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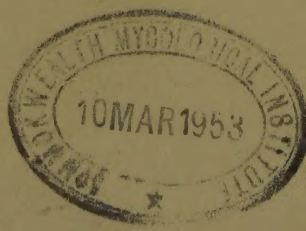
Injuries to Plants Caused by Insect Toxins. II.

WALTER CARTER 680

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HENRY ALLAN GLEASON and EDMUND H. FULLING

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EDMUND H. FULLING

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PROF. MYRON P. BACKUS
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THE BOTANICAL REVIEW

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WOUND HEALING IN HIGHER PLANTS. II¹

ROBERT BLOCH

Botany Dept., Yale University

INTRODUCTION

The organizing principle in living things controls, in some way, not only the production of many different patterns and specific individual forms but also their maintenance and regeneration under changing or adverse conditions. An expression of this is the capacity, possessed by both plants and animals, to repair injuries of different kinds and to restore certain lost portions.

In the previous review (8) the general phenomena of wound healing in higher plants have been discussed with reference to organ structure, to external conditions and to specific morphogenetic problems. These are, in particular, dedifferentiation, meristem formation, redifferentiation and tumor formation (compare 8, summary pp. 135-137). In the decade which has elapsed since, additional information has become available on practically every aspect of wound healing. There have been relatively few papers dealing with experimental work on wound hormones; the problems of cellular reactivity and specificity in plants have, on the other hand, gained wider interest. Researches in atypical growth forms and tissue cultures have attained major importance, and workers in these fields are recognizing the significance of reactivity studies for their particular materials. It is becoming increasingly obvious that many of the phenomena and atypical growth forms encountered must be interpreted in the light of experience gained from studies of regenerative processes and certain "pathologic-anatomical" tissue structures.

Strictly speaking, of course, the concept of wound healing would not seem to imply much more than the closing and scarification of a wound by means of strictly local cellular changes involving cell division, cell growth and cell differentiation, or, as in the majority

¹ Supplement to article in *The Botanical Review* 7: 110-146. 1941.

of cases, a combination of these. As it is, however, the actual processes can be neither adequately described nor properly interpreted without reference to plant structure and development and to the general phenomena of differentiation and regeneration. On the one hand, wound healing is concerned with the induction and growth of individual meristems. It poses problems of a general morphogenetic nature, for one may ask: What is it that knits together the various developmental phases in the healing of a wound in such a way that structures emerge which resemble or are even identical with those originally present?

Thus in an injured terminal meristem the original cell and tissue pattern may become fully reconstituted. Wound healing is here identical with true or direct regeneration. In other parts of the axis, but in the same plant, there may be areas in the cortex or pith which react to the stimulus of wounding by formation of wound cork or callus, or more specific cell patterns. These areas differ from the apical regions in their anatomical and physiological properties. The differences are related to the stage of development of cells located in these various areas and to their reactivity or developmental potency. Many injuries even lead, in addition to local responses, to growth reactions in places that are rather distant from the wound. They may lead to compensatory development of organ primordia, and in this manner they may involve the entire system of the plant. These reactions are of great theoretical and also of practical significance, but are usually discussed in a separate category dealing with regeneration (compare 68*a*).

Emphasis, on the other hand, will be laid on the aforementioned relationships of wound tissues to atypical growth. Familiarity with various types of wound calluses is essential for the interpretation of artificially induced and often seemingly more complicated deviations from the typical tissue pattern, as observed in tissue cultures and various kinds of plant tumors.

ORGAN STRUCTURE AND WOUND RESPONSE

STEMS. Wound repair in terminal meristems has the character of regeneration. The self-reconstituting capacity of these specific regions is well known and has been experimentally analyzed by a series of operative treatments on shoot apices. The latter have been subdivided artificially into smaller tissue units than those studied by previous workers. Wardlaw (75, 76) demonstrated

techniques by which the shoot apex of a leptosporangiate fern, *Dryopteris aristata* Druce, may be divided into four segments instead of two by making two longitudinal incisions in lieu of one. In other experiments the apical cell was punctured, or central parts of the meristem were damaged. Similar operations were subsequently performed on a higher plant, *Lupinus albus* L. (Ball, 5, 6). In some of these experiments the central part of the apical meristem remained without direct vascular connection with the main system of the shoot; nevertheless it retained high regenerative ability. Additional information was obtained with regard to the developmental potencies of other regions of the growing point.

Previously cases had been noted in which the callus of grafted woody stems was derived from tissues other than the cambium. Juliano (39) reported similar behavior for various species of *Nothopanax*; in cleft-grafted stems callus was first formed in the gap from parenchyma cells of the cortex and pith and from ray cells. From the callus a cambial bridge subsequently joined the cambial regions of the stock and scion.

Various forms of periderm formation have been studied. Klinkenberg (41) made a careful histological study of cork formation in herbaceous stems, such as *Pelargonium tetragonum* L'Hérit and *Begonia Seemanniana* A.D.C., paying special attention to processes of necrosis and the reactivity of different cell types. Brauner et al. (12) reported that potato tubers do not form wound cork at all if kept under anaerobic conditions, thus confirming earlier workers. De Zeeuw (81) investigated the influence of exposure on the time of deep cork formation in three northeastern trees, red ash (*Fraxinus pennsylvanica* Marsh), tulip poplar (*Liriodendron tulipifera* L.) and white pine (*Pinus strobus* L.). Exposed trees formed deep cork earlier than those which had been protected from direct insolation. The discrepancy was six years for red ash, five years for tulip poplar and fifteen for white pine.

The bark of aspen (*Populus tremuloides* Michx.) normally consists of a smooth persistent periderm. According to Kaufert (40), rough fissured bark may occur as a result of mechanical injury, fungi and lichens. *Macrophoma tumefaciens* Shear appears to be the most common cause of rough bark, the mycelium penetrating the layers of periderm and stimulating formation of new layers below. Mechanical injuries are apparently caused by hail, sleet or whipping of brush.

Injuries to trees caused by vines are of a different kind. Muller (63) noted that in *Celtis mississippiensis* Bosc. the vines of *Menispermum canadense* L. cause the formation of spiral lines of constriction on the bark of the host tree, along which peridermal excrescences or tumors subsequently appear. These are due to meristematic activity of small areas of phloem. The causative factor is apparently some chance mechanical injury.

Other vines which cause conspicuous injuries to stems and branches of young trees are bittersweet (*Celastrus scandens* L.) and grape (*Vitis aestivalis* Michx., *V. vulpina* L., *V. labrusca* L., and *V. bicolor* Le Conte). The injuries resulting from spiral coiling of bittersweet, for example, around the stems of *Sassafras albidum* Nutt., produce constriction of the phloem with ensuing accumulation of substances. Considerable increment takes place of radial growth above the constricting vine. However, the trees are rarely killed by bittersweet vines, since new conductive tissues are formed whose elements become oriented parallel to the spiral constrictions (Lutz, 52).

Thoennes (69) described effects on the later growth of trees of injuries caused by the cicada *Magicicada septendecim*. The egg-laying activities result in injury, apparently destruction or modification of xylem tissue.

Gilbert (31) described traumatic effects in the young stems of oaks in which there were definite signs of "reversion" to the diffuse porous condition as the result of the hypertrophy produced. Whatever the physiological conditions affecting the growth processes in the wounded areas may be, there seem to be good indications "that in this case there is definite reversion to the ancestral type of vessel arrangement". Different types of tyloses in two oak subgenera, *Erythrobalanus* and *Leucobalanus*, have been described by Williams (80).

Interxylary cork as well as formation of cork in other locations were studied by Moss (61) in various species of *Artemisia*; reference was made to their taxonomic significance.

ROOTS. Klinkenberg (41) studied periderm formation and necrotic processes in roots of various Crassulaceae and Cactaceae, and also made a detailed histological investigation of tomato plants affected with corky root. She also studied the necrotic virus spots of roots of lupine that had been affected by sore shin or Lupinen-

bräune. Numerous figures of stages of internal and external cork formation and illustrations of necrotic cell areas are given.

Fourcroy (25), in an extensive paper, described experiments with roots of *Vicia Faba*, *Ricinus communis* and *Lupinus albus* that had been injured by pricking, cutting or dipping into acids. Particular attention was paid to the way in which differentiation of the vascular system was affected by a wound near the tip of the root. As in this worker's previous communications, inhibiting effects as well as accelerating ones on the differentiation of xylem cells were observed, the former with reference to elements to be formed first in the ontogeny of the root, the latter with regard to elements normally differentiated later. This latter effect is carried to a considerable distance from the wound, and the author compares this pathological acceleration with "precocious aging", similar to the normal basifugal acceleration or progress of differentiation. Effects of the injury on tissues other than vascular systems were also studied, such as the formation of protective layers of cork meristem and of necrotic centers. The gradual reappearance of the normal structure of the root was also examined in detail. This paper also contains a study of the anatomical changes that are produced at the base of the hypocotyl of *Brassica oleracea* by a gall-forming species of *Ceuthorrhynchus*.

Continuing his studies on the roots of monocotyledons, Bloch (9) studied wound healing in the air roots of *Monstera deliciosa*. Roots injured at a sufficient distance from the meristematic apex react to the stimulus of wounding by formation of a repair tissue which is formed from older cortical cells and shows a characteristic surface-interior pattern. This pattern consists of successive layers of suberized cells toward the surface, thick-walled lignified cells beneath, and parenchymatous cells in the innermost region. Such a pattern is commonly found in plant tissues adjacent to external or internal surfaces. In *Monstera* it could also be made to form in internal locations simply by experimentally creating internal "centers" or surfaces of necrotic cells.

LEAVES AND PETIOLES. Cork spots on the leaves of various species of Crassulaceae and on leaves of non-succulent plants, such as *Gnetum Gnemon* L., *Camellia japonica* L. and *Clivia* sp., were studied histologically by Klinkenberg (41).

In leaves and in petioles of *Monstera deliciosa* wound tissues

show characteristic patterns quite analogous to those in the air roots of this plant (Bloch, 9). Welch (77) studied the progress of cicatrization in leaves and petioles of *Bryophyllum calycinum*. Sections were made immediately after wounding, after four hours, after three, four and six days, and after ten weeks. In leaves that had been removed from the plant the layers of pseudocicatrices were less developed than in those that remained attached to the plant.

Again, a number of workers have investigated various anatomical types of abscission. The process of separation of leaves and other plant organs has received much attention in the past, since it has various important theoretical and practical implications. Hilpert (37) described the processes of abscission and the closing of the ensuing wounds in flowers and fruit stalk of *Ricinus communis*. Anatomical and chemical aspects of abscission of apple fruits were studied by McCown (57), and the anatomy of leaf abscission in guayule and of experimental defoliation by means of flash-drying by Addicott (1).

Facey (24) investigated abscission of leaves in *Fraxinus americana* L., studying in particular the progressive chemical changes in the cell wall before and during abscission. It is concluded that some of these changes are associated with a natural lowering of pH in the leaves and could be induced artificially by treatment with dilute hydrochloric acid. On the other hand, retention of leaves occurred in branches which had been exposed to ammonia vapor that produced an alkaline reaction in the cells and prevented the change from calcium pectate to pectic acid.

The histological changes associated with leaflet abscission in *Phaseolus vulgaris* were studied by Brown and Addicott (13). Explants consisting of the terminal leaflet, including pulvinus and ten millimeters of the subtending leaf stalk, were used. The progressive changes were observed until abscission took place which reached its maximum on the third day. A variety of anatomical and physiological changes in pulvinus and stalk were noted, in addition to cell division and other changes in the abscission zone proper. The effects of chemicals, such as 2,4-D, were also studied. Livingston (47) described leaf abscission in the Valencia orange.

A discussion of the numerous papers dealing with different physical and chemical factors or agents, accelerating or inhibiting the abscission of leaves and other plant organs, would exceed the scope of this review. A study by Gawadi and Avery (27) is of

interest here, however. These workers carried out experiments of a physiological nature in order to determine to what extent cell divisions occurred within the zone of separation and were causally related to the process of abscission. The authors used several species of herbaceous plants, representing three types. In the first type the process of separation of the leaf is preceded by cell division in the separation zone (*Poinsettia*, cotton and pepper); in the second (*Impatiens*) there is no preformed layer of dividing cells; in the third, the leaf of tobacco, there is evidence of occasional cell division, although the leaves do not abscise naturally. It is significant that in the first group leaf fall can be induced experimentally, for example, by treatment with vapor of carbon tetrachloride or ethylene chlorohydrin, before cell divisions have made their appearance in the separation zone. On the other hand, in type II, which lacks these divisions, abscission occurs both normally and after experimental induction. It is obvious that the presence of a layer of dividing cells in the separation zone at the base of the petiole of abscising leaves is not essential for abscission to take its regular course. This layer should thus be interpreted as of the nature of periderm, ultimately forming the protective tissue of the leaf scar, a view held by many previous workers. There remains the problem of the factors normally instrumental in the induction as well as the location of these divisions in definite positions. To this reviewer it would appear that they must be related to those which control the analogous formation of superficial or internal cell divisions in tissues which later become typical periderm.

FRUITS. An anatomical examination of the brownish cork spots in the flesh of the fruit of apple varieties was made by Klinkenberg (41). These well known spots, which occur both superficially and internally, consist of small areas of necrotic cells adjacent to which normal cell groups assume the character of callus or cork.

The present reviewer made a histological examination (unpublished) of wound tissue formation in fruits of various lines of *Lagenaria vulgaris*. Both young and fairly grown fruits showed excellent regenerative ability, as demonstrated by the fact that circular plugs of fruit tissue that had been removed with a cork borer and promptly reinserted would generally fuse and subsequently reach maturity along with the rest of the fruit. This was also the case when the plugs were replaced after having been rotated into a

position differing from the original. Tissues were thus made to coalesce that originally had not been in contact with one another, indicating that there is little polarity in such fruits.

PHYSIOLOGICAL CHANGES ASSOCIATED WITH WOUND HEALING

The physiological basis of normal development and of regenerative growth and differentiation must be, of course, closely related. However, there is still relatively little known as to how sudden disturbances of the "correlative" and internal environmental equilibrium express themselves in physiological or physico-chemical terms.

Ulrich and Lafon (74) studied respiratory intensity in tomato fruits at different stages of development, as well as its increase and variations in wounded fruits of this plant. Their data confirm those reported by previous authors, and it was also found that wound respiration becomes reduced as fruits approach maturity.

It is known that mechanical manipulation increases respiration in leaves and other plant organs. Audus (4) studied, in detached leaves of cherry laurel, the role in this effect of intermittent stimulation and of leaf turgidity. Arceneaux (3) reported on the accumulation of sugar in the stalks of sugar cane that had been damaged by wind. Combes (18), supplementing his previous work on leaves, studied the effects of incisions in petals and sepals of *Lilium croceum*; transport of nitrogenous material from the perianth became accelerated. The general effects of wounding on the nitrogen metabolism of various fruits have been discussed by Ulrich (70); his paper contains, in addition to his own experiments, a review of literature in this field. The same author (71) studied similar effects in the leafy shoot of *Pisum sativum* and reported for the same material (73) on the effect of wounding on carbohydrate metabolism. He has also, in a résumé of wound reactions in higher plants (72), discussed some of the general problems of wound healing.

Marshall, Childers and Brody (55) reported that several species of apple leaf hoppers and the potato leaf hopper cause injuries in apple leaves (Stayman Winesap variety) that are accompanied by a more or less marked reduction in apparent photosynthesis and transpiration. Apple leaf hoppers generally removed the contents of the palisade cells.

Among the numerous physiological traumatic reactions, changes

of a necrobiotic kind and chemical changes of a hormonal nature appear particularly significant.

WOUND HORMONES AND NECROTIC CHANGES

WOUND HORMONES. The complex mechanism and the physiology of wound healing and regenerative growth are by no means better understood now than when the previous review was written. Like typical growth, organized wound repair consists of many components: dedifferentiation, cell division, cell growth and differentiation, as well as formation of orderly patterns. These involve a multitude of factors and processes intricately woven together. The initial phases of wound tissue or callus formation, namely, cell division and growth, are usually associated with decomposition processes in cells and with the formation of necrotic and autotoxic products, and may be related to them causally (compare 8). Such a relationship, probably of a specific chemical nature, has long been suspected, and wound substances have been isolated, termed "wound hormones" (compare 8 and 64, pp. 76-83). One of those substances previously purified, traumatic acid, is possibly an oxidation product of substances normally present in the cells and may, besides auxin, stimulate the growth and division of cells.

English (22) reported additional synthesis of a number of dicarboxylic acids other than traumatic acid which are all active to varying degrees as wound hormones.

Hemberg (34) found that in cut discs or slices of potato tubers that had been exposed to air for three hours there are formed two kinds of growth substances (*Avena* test). The first one is acid in nature and probably identical with indoleacetic acid or one of its homologues. Presumably this is formed from decomposition products of injured cells. Possibly this decomposition product serves as activator for the formation of auxin or a wound hormone of the type suggested by Haberlandt. The second substance has a neutral reaction and may possibly be indoleacetaldehyde (35).

It is known that the rooting of certain cuttings may be enhanced not only by treatment with growth substances, but also by additional wounding of the base or side of the cutting. LaRue (45) found that petioles and stems of herbaceous cuttings that had their bases repeatedly sliced showed increased rooting as compared with uninjured controls. Extracts presumably containing wound hormones were effective also.

Davis (21) tested wound healing activity in sugar maple (*Acer saccharum* Marsh) for traumatic acid, glutathione, and four growth substances, using different concentrations in talcum as a carrier. In these experiments only glutathione was found to stimulate wound healing.

Loofbourow and collaborators have continued their studies of the formation of proliferation-promoting intercellular hormones in injured yeast cells (48, 49, 50, 51), and Cook and Cronin (19, 20) have compared extracts from such cells with known bios components and amino acids.

NECROTIC CHANGES. Characteristic physiological and structural changes commonly occur in cells adjacent to wounds. The study of these changes is of considerable interest, since they are closely linked with the stepping up of metabolic activity and the resumption of division and growth in adjacent healthy cells. The formation of cork barriers, "suberized deposits", wound gum, lignin, phlobaphenes or phenolic compounds have been studied by various investigators. Often these changes render the tissue more or less resistant or immune to parasitic infection and thus form an important part of the natural defense reactions of the plant to the presence of pathogens and their toxins (compare 8 and 25a).

As has been previously pointed out (8, page 122), there are often difficulties in the interpretation of the microchemical reactions of necrotic deposits, and care has to be exercised in determining, for example, whether a certain chemical change in the cell wall is due to the presence of true lignin or of other necrotic compounds which may give a similar microchemical color reaction.

Klinkenberg (41) has illustrated a number of typical cases of tissue necrosis which occurred as a result of wounding or other pathological conditions, such as virus infection. Included is an anatomical study of those well known small necrotic "gummy" areas or "centers" which frequently make their appearance at a certain distance from the main wound surface. In sugar beet (42) it has been possible to differentiate between *Verticillium* disease, virus-yellows and an etiologically obscure necrosis, merely anatomically on account of differences in the internal necrotic changes. In *Verticillium* disease there appear dark substances first in xylem elements which then spread to surrounding tissue and to the surface of the petiole. Beets afflicted with virus-yellows show gum-

mosis of the sieve tubes, following a generally diseased condition of the phloem. The necrosis of unknown cause is not easily distinguishable from virus-yellows microscopically. In this disease there appear, however, very darkly staining necrotic compounds in the wood vessels.

The effects on differentiation of internal necrotic areas in parenchymatous tissues in air roots and petioles of *Monstera deliciosa* were studied by Bloch (9).

Hill (36) has made a comparative study of suberin and "suberized deposits" of lesions in potato tubers affected with different diseases. Simonds (65) investigated phloem necrosis, deposition of tannin-like material and other pathological changes in raspberry canes. These occurred as the result of winter-injury or of artificial injuries such as freezing, alternate freezing and thawing, or desiccation above freezing temperature. Esau (23), in studying the anatomical changes in the phloem of *Nicotiana Tabacum* affected with curly top, described degenerative changes that occurred in the apices of shoot and root; these started to appear in the cells adjacent to the first differentiated sieve tubes. Cell divisions subsequently lead to formation of hyperplastic atypical phloem. Tomato and sugar beet show the same degenerative changes as tobacco.

Metcalfe (58) reported that the watermark disease of willows is characterized by pathological changes in the cells of the wood, consisting in accumulation of oil, polyphenolic compounds, and oxidation of these to brown substances; probably this is the result of a greatly disturbed physiology caused by the presence of bacteria. That such substances frequently render the cells and thus the plant resistant to parasitic infection or penetration, has previously been shown in a number of cases. Phenolic compounds play a significant part in many instances of cellular resistance. Greathouse and Rigler (33) tested 45 phenolic and related compounds upon the growth of *Phymatotrichum omnivorum* (Shear) Duggar in pure culture and have listed the compounds in order of their toxicity.

Behr (7) reported that potato tubers which had been treated with different alcohols or with chloroform did not develop periderm, although the cells remained alive. Subsequently the tubers showed little resistance to species of *Phytophthora* and *Fusarium*.

McClure and Robbins (56) made a study of damping-off in cu-

cumber seedlings and found that resistance to infection by *Pythium* depended on a change in the walls of the cells surrounding the areas of infection, described by them as deposition of lignin.

SPECIFIC PROBLEMS

The technique of artificially induced wound healing is a useful tool for the study of specific morphogenetic problems, for example, those which have to do with the mechanism and plane of cell division, cell growth and cell dedifferentiation and differentiation. Compared with the original meristems of the plant, wound meristems generally possess much larger, easily recognizable cells with well developed walls. Such cells are much less sensitive to experimental manipulation than the small, densely cytoplasmic, thin-walled cells at the growing points.

CELL DIVISION. As is well known, the plane of cell divisions in a wound meristem is usually parallel to the surface of the wound, or vertical to a gradient in wound hormone concentration or some other factor. Other directions may also occur, especially in the later stages of wound tissue formation and in special locations (compare 8, page 128). One interesting property which characterizes early divisions in a wound meristem is the relative position in adjacent cells of cell walls which are frequently laid down exactly opposite each other (Sinnott and Bloch, 66). Commonly, in plant tissues a new wall does not meet an old one at a point directly opposite the point of insertion of an adjacent partition wall. In the majority of plant tissues the walls thus alternate or "break joints", and only three walls meet at a point. But in certain tissues, for example, in many types of roots whose cortical tissue cells show a "radial concentric" arrangement, as seen in cross section, exactly the reverse condition occurs. In early development each new wall is laid down exactly opposite the point of insertion of a previous one so that four walls meet at one point. The same occurs frequently in normal and regenerative periderm, and has, for example, been induced artificially in wounded stems and petioles of *Bryophyllum*, *Kalanchoe*, *Tradescantia fluminensis* and other plants. An understanding of the factors which control the insertion of cell walls opposite each other in wound tissues may therefore throw light on an important general character in the normal tissue pattern.

Bünning (15) has also studied the plane of cell division in wounded roots of *Sinapis alba*. In the cells of the cortical parenchyma and the rhizodermis the plane of division is such that it can be related logically to a characteristic path of transport of wound hormones from the wound surface.

In the somatic tissues of a considerable number of angiosperms there occur not infrequently cells which possess a multiple of the set of chromosomes typical for the plant. Such cells, that have long since stopped dividing, are characteristic for certain tissues or regions, particularly the periblem of roots. This phenomenon and the process of internal somatic doubling have been called rather loosely and interchangeably, polysomaty, endopolyploidy or endomitosis. The occurrence of such polyploid cells has been noted not only in normal tissues but also in wound tissues and calluses, and in certain plant tumors. In some cases the condition may be inferred from the size of nuclei and other criteria in the resting cells of the vegetative tissues. Mostly, however, some special technique, such as wounding, is required in order to induce mitotic divisions artificially and observe the number of chromosomes present in the cells. Grafl (32) demonstrated in this manner that in *Sauromatum guttatum* certain mature tissue cells were tetraploid, octoploid and 16-ploid. Geitler (28, 29) reported similar conditions from evidence in induced wound tissues in succulent leaves of *Rhoeo discolor*, and Geitler and Lauber (30) and Lauber (46) in fruits of *Liliaceae*, *Loasaceae* and *Solanaceae*.

DEDIFFERENTIATION AND REACTIVITY. Typical dedifferentiation of cells has been frequently described for plants, but it is less generally encountered in animals. Plant cells may lose, not only in wound and in regenerative tissues but also during the course of normal development, their differentiated character and become more embryonic and less specialized. They, at the same time, show changes in metabolic activity and protoplasmic character. Resumption of cell division and wall growth are frequently followed by functional and structural metaplastic changes which indicate that the cells have undergone a process of redifferentiation. The concept of totipotency or pluripotency has long been familiar to botanists (compare 8). The rather unstable determination of cellular character in plants, as compared with those of animals, has also not entirely escaped the attention of experimental plant mor-

phologists, although it has been mentioned only rarely. A statement made by Küster in 1903 (44, page 299) appears significant in view of the recent revival of interest in this field. Referring to the fact that in atypical growth any kind of tissue may give rise to any other type of cell or tissue, the view was expressed that in plants there is no "specificity of tissues", such as seems to occur in animals. At the same time Küster recognized that the different behavior of plant and animal tissues may be explained on the ground that the differentiation of the latter is predominantly determined by internal factors and relatively little affected by those changes in external factors with which we operate in our experiments.

In normal ontogeny the different histological character of cells in different positions in the plant body is in many ways tied up with factors in the environment. It is therefore not surprising to find that many potentially meristematic cells will exhibit considerable pluripotency whenever inhibiting correlative influences can be removed and external factors may once more conspicuously affect the physiological state of the cell and regulate its growth activities in a variety of ways. Most effective experimental methods which will bring about such changes are wounding and isolation of tissues or organs, culture of tissues, and growth substance treatment.

There are, however, differences in the reactivity of plant cells to the stimuli which induce dedifferentiation, and wounding is a convenient method with which to demonstrate this differential behavior of plant cells in relation to their age, position within the plant body and their histological type (9). There are differences in their readiness for division and renewed wall growth, although both are very commonly seen in cells of the parenchymatous and collenchymatous type. Relatively differentiated cell walls may resume active growth in surface and in thickness. During the process they sometimes lose their impregnated character. To the present reviewer there appears little doubt that the study of the fine structural changes of such extending cell walls in wound meristems and calluses can provide valuable information about the processes of cell wall growth in general and about certain aspects of wall nomenclature in particular. It is in itself a remarkable fact that the walls of cells which have long ceased growing and dividing should be able to undergo reversible changes or renewed growth under the

altered conditions that prevail in wound meristems. This is not surprising, however, when one considers that, for example, in the normal development of collenchyma cells the major part of extension in the young wall actually occurs long after the onset of wall thickening. According to the old nomenclature the thickened part of the wall is "secondary wall", and its formation was believed to follow the primary phase of extension and growth in surface (Majumdar and Preston, 54; Majumdar, 53).

The method by which the growth in surface of the wall of cells takes place within the callus or wound tissue is most probably one of active intussusception in which the protoplasm itself plays an active role. Often this growth is limited to certain parts of the cell, for example, its ends. This general concept of surface growth of walls has been supported by electron-microscopical evidence in primary cell walls (Mühlethaler, 62).

Cytological aspects of cell and tissue dedifferentiation have been studied by Buvat (16). In an extensive paper there are surveyed cases of dedifferentiation in normal and regenerative development, augmented by new investigations. These deal in part with adventitious root formation in the stem of tomato and with vegetative propagation of leaves of *Brimeura amethystina* L. Besides histological development of regenerating organs, various phases of dedifferentiation have been studied, with emphasis on nucleus, plastids and chondriosomes within different cell types. Another part of the paper describes dedifferentiation in parenchymatous tissue cultures of *Daucus carota* L. and in tissue cultures of the tuber of *Cichorium intybus* L., also including similar cytological studies. Finally changes were studied in stems of tomato that had developed crown gall. This investigation fully confirms those observations of previous investigators who had noted that in processes of regeneration cells of very different origin, type and location may dedifferentiate. The author gives numerous details of the changing cytological structures of cells, especially of the chondriom, in the various phases of regressive development. He concludes that, in contrast to animal cells, no plant cell is irreversibly determined. In his opinion every cell in an angiosperm, unless degenerated, can more or less dedifferentiate under the proper conditions. "Elle est toujours capable de se remettre à proliférer, de perdre ses caractères structuraux de spécialisation et de se spécialiser différemment par la suite" (16, II. pp. 103/4).

The conclusion of this investigation thus supports the previous one reached by Küster and other workers. Whether it would be tenable in such a generalized form, however, will, in the reviewer's opinion, depend on further comprehensive experiments with a greater variety of physiologically different types of cells. Certain observations of developmental as well as experimental nature seem, at least at the present stage of our knowledge, to suggest that some caution may be indicated. It appears, for example, rather remarkable that there are no clear and convincing observations available which would show that the various types of physiologically specialized cells of so-called idioblastic type undergo full de-differentiation in wound tissues. Many of these cells contain oil, tannin or other secretory material, such as crystals. A study to ascertain the behavior of one type of such cells has been made in *Ricinus communis* (10, 11). In the stem of this plant there occur secretory cells whose contents give the reactions of unsaturated fats and tannins. These cells acquire the specialized cytoplasmic character very early in development and transmit it to their daughter cells. In wound tissues, as well as in tissue culture, cells of this type, which have stopped dividing within the mature zone of the internodes or nodes, resume both division and growth along with the rest of the cells of the ground parenchyma. They do not, however, lose their special cytoplasmic character during this process. Apparently the properties which distinguish them from the rest of the parenchyma arise originally as a result of so-called differential divisions, that is, they are, in the last analysis, determined internally. It appears only natural, therefore, that secondary changes in external conditions or in the intercellular correlative position of the cells within the plant body do not easily affect their cytoplasmic character. Nevertheless, under proper conditions the cells still reveal the potentiality of division and growth along with the rest of other living tissue elements.

Another example of cells undergoing early functional segregation from the rest of the tissue cells has been reported by Meyer (59). In the leaf of *Urtica dioica* the cystolith cells are rather stably determined. In leaves affected with galls caused by *Perrisia Urticae* these cells undergo modifications according to their new position in an atypical location. In the hair-bearing region of the stomatal openings hair-shaped cells are found which contain, however, cystoliths. On the other hand, in the region of growth, rows of

cystolith cells occur; these arise by transverse and especially by longitudinal divisions which are characteristic for the epidermal layer. Here, as in other cases, the character of cells may be considerably modified by cecidogenesis, but the potency for the differentiation of cystoliths is determined in these cells at an early stage and is not lost. It is significant that cystoliths are formed only in those daughter cells that have arisen as a result of longitudinal divisions, for only then does each daughter cell obtain a part of the external cell wall in which the potency for crystal formation resides.

There are other indications that the various forms of cellular and tissue determination and of modification which occur during the course of normal differentiation within a plant differ in degree of stability and reversibility; this has been suggested also by Bünning (14). Of those modifications initiated by external agents at least one is well known that appears irreversible under conditions of regeneration and tissue culture, namely, the secondary tumor cell type attributed to the action of *Bacterium tumefaciens*.

DIFFERENTIATION. The accelerating effect of wounding on metabolic activity and on visible cell and tissue differentiation has been previously discussed (8). Fourcroy (25) studied these processes, especially as they affect differentiation of the vascular system.

One phase in the redifferentiation or reconstitution of the original tissue pattern is the thickening of the walls in cells or specific layers of cells near the wound surface. Many examples are known. In the development of the periderm of potato the first histological change of this kind is apparently a slight thickening in the outer walls of cells located in the third or fourth layer below the wound surface. Brauner et al. (12) noted that the thickened wall is present as early as 24 hours after wounding, that it stains with Sudan III and Safranin, and soon resembles an "internal epidermis".

In the roots, stems, petioles and leaves of *Monstera deliciosa* reconstitution of more complex dermal tissue patterns is common. Generally these patterns have a relation to the developmental potency of the tissue cells at the time of wounding (Bloch, 9). One remarkable feature is the differentiation of thick-walled "hypodermal" sclereids. These sclereids always differentiate be-

low a surface in a characteristic position where special external conditions must be effective.

Redifferentiation of vascular strands in wounded organs has also been investigated by several workers. Jost (38) studied regeneration of xylem bridges in *Fittonia argyromeura*, *Saintpaulia ionantha* and *Elatostemma sessile*. He confirmed the older observations of Simon and Freundlich and noted that the regenerating strand formed mostly in a polar fashion from the upper margin toward the lower part of the cut; sometimes it followed the outline of the wound. This process was studied also by Sinnott and Bloch in several herbaceous plants, especially in the stem of *Coleus hybridus* (67, 68), from the point of view of the finer but still microscopically visible changes within the protoplasm and cell wall. The new bundle connections which developed across the pith included both phloem and xylem strands. The latter consisted in part of elongate tracheids and vessels formed from procambial divisions parallel to the course of the new strands, and in part of vacuolate and nearly mature parenchyma cells which differentiated directly into spiral and reticulate xylem elements without previous division. In these cells the configuration of the lignified bands had a definite orientation relative to the axis of the new strand, and this re-orientation became evident first in the cytoplasm of the cells. This cytoplasmic pattern of bands and its final manifestation in the lignified thickenings are not independent configurations in each cell, but form a harmonious coherent pattern extending across a group of cells, the bands in one cell being directly continuous with those in adjacent ones. The evidence suggests that histological differentiation, both normally and in regeneration, frequently involves the establishment and operation of such intercellular fields or patterns in the cytoplasm of groups of contiguous cells.

This reviewer has always been impressed by the relative ease with which fundamental parenchyma cells can be made to differentiate into tracheid-like elements. This may be observed in many instances of regenerative as well as of pathological growth. This type of cellular metaplasia very commonly observed in calluses, tissue cultures and tumors, requires relatively little change in the fundamental character of the cell, involving only deposition of specifically arranged "secondary" wall material.

From a discussion of this phase of research in regenerative differentiation the significant observations made by Camus (17) should not be omitted. In order to analyze the promoting influence

of buds on the formation of roots, grafts were carried out in which the buds acted as organizing centers. These induced processes of dedifferentiation and subsequent redifferentiation of vascular strands in the stock tissue onto which they had been grafted. That an organizing principle from the buds is able to pass through the region of the graft could be demonstrated even more strikingly by placing a bud on an isolated piece of tissue taken from the root of *Cichorium intybus* L. These tissue fragments consisted of old cells of vascular parenchyma only, and it was found that under the influence of the bud such old parenchyma cells would dedifferentiate and redifferentiate into groups of conducting elements. The presence of considerable potentialities in cells normally at rest is here quite evident.

In many roots there are two kinds of cells in the superficial layer, those that develop root hairs and those that do not. It is known that under a variety of conditions all cells can be made to form root hairs. Bünning (15) has shown that in *Sinapis alba* the root hair cells readily divide as a result of wounding and that the cells which do not normally bear root hairs may develop them if the superficial layer of the root is partly isolated by short longitudinal incisions.

The preceding examples of redifferentiation strikingly demonstrate the pluripotency of parenchyma cells which may undergo metaplastic changes either directly or after dedifferentiation. However, as previously discussed, there are exceptions. These are, on the one hand, highly differentiated cells in which wall incrustation and other cellular characters are very pronounced and a physiological state of senescence is present. On the other hand, there are those cells of idioblastic type in which physiological specialization is rather stably determined, as in the secretory cells of *Ricinus* or the cystolith cells of *Urtica*.

ATYPICAL GROWTH. When tissue patterns arise which, either spontaneously or in reaction to traceable causes, differ conspicuously from the normal, or when even a lack of pattern is encountered, we speak of atypical growth. Examples are some large caluses, tumors of various kinds and forms obtained in tissue cultures. The interest in the study of such atypical growth forms in plants has greatly increased, mainly in relation to the pressing problem of malignant growth (compare de Ropp, 21a; Gautheret, 26; White, 78, 79).

Aside from this, the study of wound tissues and regenerative

wound calluses, on the one hand, and the study of bacterial and chemical plant tumors and tissue cultures, on the other hand, are related in more than one way, and the results obtained in these fields mutually supplement each other. Thus in plant tumors and in cultured tissues certain histological changes differing conspicuously from the normal can often be interpreted on the basis of similar structures formed in ordinary wound calluses and under simpler growth conditions. On the other hand, there is hope that the techniques of growth under experimentally controlled conditions of isolated cells and pieces of tissue may bring some of those problems nearer solutions which have to do with the processes of proliferation, differentiation and organized growth in normal and regenerative development. It is very difficult to analyze in the intact plant the physiological and physicochemical events which lead, for example, to cellular diversity. In tissue cultures the experimental approach to this problem appears in certain respects more simplified, and at least some of the factors which may channel the differentiation of cells and tissue into certain directions are now being analyzed by varying the conditions in the culture medium.

In the numerous discussions on atypical neoplastic growth forms that have been compared in some way with malignant "cancerous" growth, it has become customary to employ both physiological and morphological criteria. More or less spontaneous but subsequently persisting changes in the physiology, the growth rate and the histological pattern of plant tissues would seem to indicate a fundamental alteration in cellular behavior and in the typical tissue organization. Such change has by some workers been compared with those alterations in cellular reactivity and specificity which are encountered in animal cancer. Occasionally the diagnosis "plant cancer" is based predominantly on anatomical features, involving alterations in the histological pattern, such as differentiation of centers of tracheids, formation and irregular distribution of organ primordia, or other kinds of abnormal arrangement of tissue constituents, suggesting a loss of the typical organization. It is here that a critical evaluation of the observation becomes indispensable, for the anatomical changes that are encountered in tumors formed by various chemical treatments, by virus or bacterial infection, are often strikingly similar to those seen in wound calluses and related structures. In many instances, therefore, the pathological-anatomical character of the tumors may be interpreted as merely a so-to-

speak "exaggerated" manifestation of the same histological changes that occur in ordinary wound calluses. As a matter of fact, not infrequently a relatively simple change in external factors may modify the process of wound healing in such a way that quite substantial atypical tissue proliferations result.

Similarities and analogies between calluses, tumors and cultured tissue forms occur in various developmental phases. In healthy plants hyperhydric conditions may produce formation of intumescences and tissue proliferations which closely resemble those changes that occur in the first phases of tissue cultures. After infection with *Bacterium tumefaciens*, the first stage in the formation of crown gall tumor are cell divisions resembling localized wound reactions. Isolated nests of twisted tracheids as well as irregularly located cambial activities associated with differentiation of vascular strands are often seen in large-sized regenerative calluses of herbaceous and woody plants. They have been reported also for many tumors of etiologically quite different origin, and in tissue cultures. It is known that some plants, when wounded, form cambia whose activity becomes atypical in that they produce xylem toward the outside and phloem toward the inside. Such inversion of cambial activity has been observed also in tissue cultures of the same material, for example, in *Vitis* species (compare Krieg, 43; Morel, 60).

It will not be easy, therefore, to diagnose, on mere histological evidence, a conversion from one type of growth to another one which might be called "unrestrained", since the different forms, as we have seen, are rather closely related in anatomical respect. Additional criteria, physiological and morphogenetic, are obviously required.

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INJURIES TO PLANTS CAUSED BY INSECT TOXINS. II¹

WALTER CARTER

Pineapple Research Institute of Hawaii, Honolulu

INTRODUCTION

The author's first review of the literature on plant diseases caused by the toxic feeding of insects included the available references up to and including 1938. This supplement, having been delayed for various reasons, brings the review up to the end of 1950.

The order of presentation has been slightly changed to avoid arbitrary separation of effects produced by one group or species of insect. For example, the effects of leafhopper feeding, whether they be leaf spotting, hopperburns or systemic effects, are all included under the heading "Cicadellidae". An exception to this is the section on insect galls.

The whole field of inquiry suffers somewhat from deficiencies in clearly defined criteria whereby toxins can be established as causal. Many writers simply describe symptoms, without discussing the nature of the causal entity. Others have difficulty in separating traumatic effects from those caused by toxins. These two are probably often closely associated. Several careful studies, however, seem to have established the toxic nature of insects' feeding.

With some groups of insects, notably the Capsidae, the effect of the insects' feeding appears to be so violent that mere trauma undoubtedly can be discounted. These groups appear to be increasingly important on many cultivated crops.

Certain fundamental considerations appear to have received some attention. The similarity of certain feeding effects to those achieved by hormonal action, the effect of host feeding sequence in conditioning secretions, and the similarity between certain gall-producing substances and neoplasma-genic substances indicate that this field of inquiry may contribute to the study of neoplasms as well as to the broader field of evolution.

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Allen (1947) reviewed the relationship between insect damage and plant hormones. He suggests that insects may affect the activity of response to growth substances either by injection of materials or by withdrawal of them. The relation is indicated by the similarity in growth changes in plants caused by hormones and insect feeding, the similarity in enzymic activity, and the suppression of insect damage in certain plants after treatment with hormones. Abscission caused by the feeding of the tarnished plant bug is prevented by application of alpha naphthalene acetic acid so that possibly the insect in feeding produces an auxin inactivator or interferes in some other way with the normal supply.

CAPSIDAE AND LYGAEIDAE

Injury by capsids to cultivated crops is widespread and sometimes a limiting factor to plant growth. The conclusion that toxic secretions are responsible for the injury is based largely on the very small number of insects involved and on the usually extreme rapidity with which lesions develop. In the few cases where histological studies are reported, however, the toxin hypothesis has been supported.

The extreme measure of control necessary is indicated by Lepellety (1944) who recommends that control measures be instituted when the population of *Lygus* reaches four or five per coffee tree.

Baker et al (1946) have described the effect of *Lygus* feeding on lima bean in California. This effect, which cannot be distinguished by symptoms from a disease caused by yeast (*Nematospora*), has been shown to follow the feeding of *Lygus* in the absence of pathological organisms and is ascribed by the writers to a toxin. The seeds are pitted, and shedding of blossoms and small pods with some shrivelling of young seed occurs. This is one of the few instances where an effect of pathological primary or secondary organism has been eliminated as a prelude to the conclusion that a toxin is involved.

Lygus vosselvi (Simoni) Popp as a cotton pest in Uganda has been reported in some detail by Taylor (1945, 1947). Taylor stocked cotton plants with 25 *Lygus* nymphs and repeated this at intervals of two weeks. His comparisons were then drawn between infested plants and controls which received more than "normal" infestation and were considered severely damaged. The

differences between these two sets of plants, representing two types of infestation, were pronounced enough to indicate that the effect of either the total population or the regular increments of fair-sized populations was most pronounced. These differences are shown in Table I.

Taylor's account of the immediate reaction of tissues to *Lygus* attack is in contrast to the effects of prolonged infestation. Black spots appear within three hours after feeding, and the cells in these spots are dead. His observation that because such spots, when on leaves, are bounded by veins, the mechanical or toxic action can

TABLE I

Heavily infested at intervals	Field incidence considered severe
Columnar in shape, owing to shortness of all branches	Conical; the lower branches, including the lower sympodia, being much longer
Very ragged in appearance	Much more normal
Primary sympodia averaged 2.1 nodes	Primary sympodia averaged 3.1 nodes
Internodes on main stem and branches often very short so that leaves bunched	Internodes mostly normal
Many abnormal secondary, tertiary and axillary branches, all weak and useless	Comparatively few abnormal branches
No. of bolls that persisted was 6 & 4	No. of bolls that persisted was 21 each
All bolls unhealthy and useless; crop completely destroyed	At least 10 bolls per plant appeared healthy and likely to mature

not penetrate veins, should perhaps be supported by histological evidence that the insect does not penetrate veins in its feeding.

More important, however, is his observation that it is necessary for the matter of mechanical or toxic damage to be cleared up if resistant varieties are to be evolved. His own conclusion that the damage is primarily mechanical and secondarily toxic would imply that the mechanical damage resulting from action of the stylets is a court of entry for the toxins of the saliva. The fact that many other capsid species cause the same type of injury is not necessarily in favor of a purely mechanical damage. These insects are all closely related taxonomically; there is no reason to suppose that certain elements of their salivary secretions are not also related.

In Taylor's discussion of the possibilities in developing resistant varieties, it is concluded that the best possibility lies in some physi-

cal character that would actually prevent insertion of stylets or hinder oviposition.

Lygus oblineatus Say is responsible for a disease of peaches known as "cat-facing", in which bare sunken areas that become rough and corky are produced (Woodside, 1946, 1946a; Fenton et al, 1945). There is no evidence, however, of any specificity, since many other Heteroptera, notably the stinkbugs, cause the same general condition.

Lygus praetensis L. is also recognized as a pest of apple, on which it causes dimpling of the fruit (Hammer, 1939), and of peaches (Ross and Putnam, 1946). On celery, Richardson (1938) indicated toxic effects arising in the cells surrounding a puncture. This is further complicated by the insect serving as a vector of soft rot (*Erwinia caratovora*).

The effect of *Lygus* on seed production and growth of guayule in California is to reduce both the weight and viability of the seed; and when feeding occurs on the current season's shoots, both subsequent growth and flowering are inhibited (Romney et al, 1945). This study was followed by anatomical studies on infested guayule (Addicott and Romney, 1950). Ten days after infestation of young vegetative plants of guayule by 25 *Lygus hesperus* Kgt., the branch tips were gray and withered, with the stem apex and surrounding young leaves severely shrunk. Sections through the infested areas showed complete collapse of tissues near the stem apex. Behind the stem apex, areas of collapsed cells were interspersed with areas of intact cells. This last observation is no doubt the reason for the conclusion by Addicott and Romney that a toxic injection is involved. It appears to be localized to the feeding area, although presumably not to the feeding point.

Carlson (1940) described *Lygus* damage to alfalfa in relation to seed production. A mechanical localized damage to buds is caused by feeding punctures and lacerations of *Lygus*, but the rapid disintegration of buds following the traumatic injury is believed due to toxic secretions. Rosetting, characterized by development of racemes of buds near the tips of main stems and branches into disk-like clusters, follows heavy *Lygus* infestations. On the vegetative buds there is retardation of growth and a tendency to extensive branching. After removal of *Lygus*, evidence of recovery becomes noticeable within ten days.

Stitt (1940, 1944) determined the positive correlation between

Lygus species and damage to seed production of alfalfa, and in a comparative study of three species determined that *L. hesperus* was the most damaging.

In the western United States, Sorenson (1946) found that *Adelphocoris superbus* and two species of *Lygus* are important factors in the reduction of alfalfa-seed yields, with *Adelphocoris* being the most important because of its capacity to produce damage with relatively fewer numbers. This paper reports on what is essentially a control study. DDT proved effective, but the problem is complicated by such factors as the effect on bees and on predaceous or parasitic insects as well as on the forage value of the by-product hay crop.

Hughes (1943), in a detailed study of *Adelphocoris lineolatus* (Goeze), records that these insects, when seeking food, puncture buds, flowers and young shoots. This injury is believed to be phytotoxic as determined by histological studies of injury. Abscission of single flowers is the localized effect limited to one flower but not spreading to the raceme. Cell disintegration occurs around the feeding puncture and spreads through the ovary wall to the ovules.

Knight (1941), in an inclusive study of this group of insects in Illinois, reports *Lygus oblineatus* Say causing cat-facing of peaches and dieback among shoots. *Neolygus communis* Knight may leave its natural food plant, which is dogwood, and breed on pear trees, causing the fruits to grow knotty and malformed. Nymphs of the species *Psallus seriatus* Reut. feed on cotton, causing small flower buds to drop and sometimes cause the plant to grow tall and spindly.

Lygus bug injury has been studied quantitatively by MacLeod and Jepson (1942) and histologically by Jepson and MacLeod (1946). They report that, while disintegration of the tissue was limited to a small area around the stylet punctures, there were large areas of cell disintegration of terminal and lateral bud primordia, indicating retardation of growth with the lateral bud in the process of substitution for the injured terminal region.

Two species of *Amblypelta* have been described as serious pests. One, *A. lutescens* Dist., is known as the fruit-spotting bug in Queensland where it damages many kinds of fruit, with papaya the most seriously affected economic plant. On papaya suppression of normal growth results in a dense bunch of leaves with short dis-

torted stalks and very short internodes. Fruit setting is not affected, but green and ripe fruits are spotted, each feeding puncture being marked by a depressed lesion one-eighth inch or more in diameter and dark brown. On many other hosts growth abnormalities are not common, fruit spotting being the more characteristic symptom. Only very small populations are necessary to produce serious damage on papaya; one or two bugs per tree will distort the growing points within a month after feeding has started. Nymphs appear to be more injurious than adults, although this may be a matter of the relative mobility of the two forms (Sloan, 1946).

Brimblecombe (1948) found that *A. lutescens* would kill and wilt the young shoots of macadamia nut trees. Young nuts would fall prematurely with the feeding puncture visible in the shell as a watery white spot. Premature falling of the nuts is usually the first indication of infestation. If alternative food plants in the vicinity are infested, they should be destroyed or similarly sprayed with DDT.

A. cocophaga China, described by Phillips (1940) as the cause of immature nut fall of coconuts in the Solomon Islands, is also an extremely toxic insect. One or two per tree can render an area non-bearing. Such low economic populations greatly complicate the control of these two species of *Amblypelta*. Phillips believes that direct control methods are impractical. He indicates that the only remedial measure possible is biological control. Biological control of such an extremely low population, however, would be unlikely.

Studies on control of *Helopeltis* on cacao and cinchona have been made in Java, the Belgian Congo and East Africa. Betrem (1940, 1941) found that when 80 adults of *Helopeltis* are to be found on 100 bearing cacao trees, control measures should be instituted. He recommends frequent light dustings of derris dust. See also Verbeek (1942). In view of the recent developments in residual insecticides, control measures can probably be materially improved.

Lefevre (1942) believes that dusting against *H. orophila* on cinchona is a surer control than either biological control, which is spasmodic, or hand picking, which neglects the immature forms. Kirkpatrick (1941) used a poisoned-bait spray of sodium arsenite

and sugar to control *H. bergrothi* vars. on cinchona in Tanganyika. Because 85 lesions were produced on the average by a single 3d instar nymph, the author believed that one adult and one or two nymphs per tree are sufficient to cause serious damage. Nymphal feeding a few minutes after hatching produces small but typical lesions. DDT sprays containing 0.125% DDT proved effective for control of *Helopeltis theivora* on tea plants, but gammexane imparted an undesirable taint to the manufactured tea (Harrison et al, 1948).

One of the most widespread and economically significant cases of capsid injury occurs on cacao in Nigeria and the Gold Coast. Voelcker and West (1940) described *Sahlbergella* blast as a major contributing cause of die-back in cacao, two species (*S. singularis* Hagl. and *D. theobroma* Distant) being concerned. Nicol (1945) summarized the data up to 1945 for the Cocoa Conference in London. Since that time progress reports have appeared regularly in the Annual Reports of the West African Cocoa Research Institute. The summary presented below is drawn, however, from a typescript manuscript by Nicol (1947).

The two species concerned (*Sahlbergella singularis* Hagl. and *Distantiella theobroma* Distant) have apparently transferred from native host plants in the west African cacao-growing areas to cacao. The difficulty in finding alternate hosts suggests that this transfer has been almost complete. Nicol described the damage for both species as due to injection into the plant of toxic materials which kill the plant cells for some distance around the punctures that the insects make. Discoloration of the area occurs immediately after puncture, going rapidly from the initial gray area to the typical brown or blackish spot. Numerous punctures involve death of the leaves and shoot. The dead leaves remain hanging on the stems for some time, giving a scorched or blasted appearance to the tree.

Damage to young cacao can be so serious as to prevent establishment of new farms. On mature cacao the attack is seasonal and when extensive gives rise to "capsid blast". Injury to small localized areas can be continuous, producing what are known as "capsid pockets". These usually are initiated when injury to the cacao tree, often by a falling forest tree nearby, results in flushes of new succulent growth which are favorable hosts for the capsids.

This new growth dies back, new shoots arise and the cycle proceeds until the trees are dead.

Nicol, in this same report, has also described *Helopeltis* damage on cacao. The pod damage is quite characteristic. Black spots developing from the feeding punctures are smaller than those caused by other capsid species and are scattered all over the pods. There has been evidence that *Helopeltis* spp. in the Gold Coast are developing a tendency to attack the vegetative parts of the plant more frequently than in the past (Nicol, 1950).

Nicol (1950) presents quantitative data on capsid populations, from which it is clear that extremely small numbers of these insects can cause serious damage. The numbers of feeding lesions for the species *D. theobroma* produced in a single day during the 5th instar varied from 13.80 to 26.20, but individual insects produced from 35 to 50 lesions per day.

Nicol has also developed an interesting and effective control for capsids on cacao, based on the habit of the insect to move into the crotch of the tree. By painting this area with a DDT emulsion, very satisfactory control has been achieved.

Pescott (1940) records another capsid (*Megacoelum modestum* Distant) on stone fruits in Victoria, New South Wales.

In Nova Scotia, Pickett et al (1944) record a fruit-malforming mirid (*Calocoris norvegicus* Gmelin) as damaging strawberry fruits.

Yellow to whitish spots caused by the feeding of *Tenthecoris bicolor* can seriously damage orchid leaves and sheaths to the point of defoliation and death (Ossiannilsson, 1946). *Tephrosia* extracts have been successfully used in Brazil against this insect (Occhioni, 1946). In Hawaii a single infestation, discovered in a quarantine house, was completely eradicated by heavy applications of wettable DDT (unpublished).

According to Usinger (1945), *Neoborus illitus* Van D. is the most serious pest of ornamental plants in California. The nymphs feed on the opening buds and later on the new growth and stems. White spots follow leaf feeding, then browning and curling. Feeding on stems causes terminal wilt of branches and finally a curling and drying of all new growth. Usinger describes a series of insecticides and ovacides whereby control can be obtained.

The Rutherglen bug (*Nysius vinitor* Berg) causes damage to

potatoes (Greaves and Rochford, 1946). There is evidence of varietal susceptibility. A quantitative method of estimating damage covered five ratings, from unaffected to dried out. On the basis of this rating, ten of 58 varieties showed little or no injury. Significant reductions in yields were associated with bug damage. No hypothesis is offered on the nature of this resistance.

The apple redbug (*Lygidea mendax*) and, to a lesser extent, the dark apple redbug (*Heterocordylus malinus*) cause a reddish stippling of leaves and a gnarling and russetting of the fruit (Dean and Chapman, 1946).

PENTATOMIDS

The role of salivary enzymes in the pentatomid *Eurygaster integriceps* and the relationship of these to wheat injury has been described by Kretovich (1943). Injured wheat contains highly active proteolytic enzymes, and the amylase in these grains is more active than in uninjured wheat. There is an interesting host tissue feeding sequence in this case. When the insects fed on leaves and stalks prior to heading of the grain, extracts of their salivary glands and foreguts displayed a strong amylolytic action, and that from the foregut a proteinase, but extracts of these did not impair the gluten flour from uninjured wheat. The salivary glands of adults fed on the ripening grain, however, yielded extracts in sodium carbonate solution which completely destroyed the gluten of normal wheat flour. It would appear that the ripening grain provided a nutritional substrate which permitted the insect to develop the capacity to destroy the gluten.

A new disease, apparently caused by the feeding of the pentatomid *Chorochroa sayi* Stal, has appeared in the potato fields of northeastern Colorado (Daniels, 1939). Cage experiments at the Greeley Potato Experiment Station with plants known to be free from psyllids and disease have demonstrated that Say's pentatomid, feeding on plants, is definitely responsible for the condition. The feeding may cause a complete wilting of the leaves or tips of the plants. Where the feeding is confined to the stems of the lower part of the plants, the symptoms become more general. Associated with the feeding is the basal curling of the terminal leaves, a yellowing followed by a reddish discoloration along the margin, and an erect condition of the affected foliage. The tubers may be produced in chains, or in the more mature tubers serious bumpiness

and malformation may occur. The number of insects on each plant determines the severity of the disease. In the Morgan County area, an average of 11 adult insects was found on each plant. Plants attacked by three or four insects were only mildly affected, while those on which there were 19 or 20 adult insects showed extreme symptoms. The disease is very similar to psyllid yellows caused by the tomato psyllid (*Paratrioza cockerelli* Sulc.). Monroe and Butcher (1940) record an extremely severe outbreak of this insect on 10,000 acres of wheat and flax.

Antestia bugs on coffee (LePelley, 1942) will cause economic damage with four insects to the tree, and only one insect per tree is necessary in some cases. The drop of green berries is not due to injuries to the stalk but to a plant response to the interruption of normal growth caused by insect feeding. This is another datum indicating that some insect secretions are similar in effect to plant hormones. Other injuries are scarring and distortion of the leaves, the non-setting of flowers and multiple branching which may result in bunchy or matted growth.

Hendrickx (Leroy et al, 1942) described a new type of *Antestia* injury as partial castration of flower buds.

ACARIDAE²

The disease of oranges known as *Lepra explosiva* is described by Vergani (1944) as a result of mite-injected toxin. Infestations of healthy oranges with the mite produced the first lesions after two to two and one-half months. The disease is local. It has not been transmitted by grafting or by inoculation of the juice of macerated mites, or by juice expressed from lesions. The disease is shown to be caused by toxins produced by this mite, since it is incapable of reproducing itself in the plant tissues; it is quickly remedied by a single application of an acaricide, and it is diminished in direct proportion to the degree with which the mites are controlled.

The redberry disease of blackberry (Essig, 1925) has been reported as widespread in New Zealand, having first been found there in 1946 (Hamilton, 1949).

THYSANOPTERA

The toxic feedings of thrips has been described by Kratochvil and Farsky (1942). As pointed out by Sakimura (1947), this is

² See also INSECT GALLS.

the first mention of thrips-produced toxin resulting in malformation of young shoots. The condition had previously been attributed to mites, other insects, fungi and virus.

APHIDIDAE

Separation of toxic effects of feeding by aphids from those involving only the simple draining of cell sap are rarely documented. Usually, toxic effects can be ascribed to small populations, sometimes as low as one or two per bush or tree, or to the short-period feeding of relatively larger populations. West (1946) provides quantitative evidence on the effect of aphid populations on the weight gains of tomato plants grown in artificial culture solutions. On ten plants an initial population of 1,000 aphids rose to 16,306 in 21 days and reduced weight gains by 38%. In another series an initial population of 851 developed to 8,894 in 12 days and permitted weight increase of 4.66 times initial weight compared with 14.7 times increase in the uninfested check. West concludes that 40 or more aphids per gram of tissue constituted a critical infestation, but presumably he means initial infestation. The enormous reproductive capacity of the aphid species used (*Macrosiphum solanifolii* Ashm.) makes length of feeding time the most significant factor. These data would be interpreted as indicating the effects of large-colony effects on available food material, and the paucity of the root systems of the infested plants would support this. These results could be compared with those of Carter (1948) where approximately equal initial but gradually reducing populations of mealybugs fed for ten days materially affected the final weight of pineapple plants after an insect-free growing period of three months.

Hildebrand (1938), in a study of the strawberry root aphid (*Aphis forbesi* Weed), found a certain amount of disintegration of cells surrounding the tip of the insect's stylet tract, but he did not consider this in itself of sufficient importance to justify ascribing any toxic action to it. Damage was related to reduction of water supply, to interference with translocation (the insect is a phloem feeder) and to disturbances of metabolic equilibria, rather than to direct injury by the insects' feeding. The last-named effect, however, might well be more deep seated than appears.

Nysterakis (1948) suggested that differences between healthy plum tree stems and those infested by *A. helichrysi* are due to the

indole-3-acetic acid inoculated by the insects. Infested stems showed higher nitrogen, protein, phosphorus and potassium than the uninfested stems.

Severin and Freitag (1938) report the curling of celery leaflets by *Aphis gossypii*, yellowing and chlorosis by *Cavariella capreae* Fabr. and white spots by *Myzus convolvuli* Kalt. All these symptoms affect only the leaves on which the aphids fed, the new leaves produced after removal of the aphids being normal.

Similarity of symptoms between feeding of the foxglove aphid (*Myzus convolvuli*) with those of lily rosette virus and lily mottle virus have been cleared up by Smith and Brierley (1948). Since neither of the viruses mentioned is carried by the aphid, the downward curling of the young foliage and irregular mottling of the old must be attributable to the feeding injury. The same species of aphid is perhaps responsible also for a lily disease in Ceylon referred to by Gadd and Loos as due to cucumber mosaic virus.

ALEURODIDAE

Dislocation of the carbohydrate and protein balance of cotton in the Punjab is an effect of attack by *Bemisia tabaci* Gennadius. Higher moisture content, lower C/N ratio, higher nitrogen content of the bolls until late in the season, and greater translocation of N, ash and fat from vegetative to reproductive organs characterize the uninfested plant. These results were in the absence of the virus diseases known to be transmitted by this insect (Husain and Trehan, 1942).

INSECT GALLS

A coccid forming galls on *Eucalyptus gomphocephala* in Western Australia has been described by Short (1947). Male galls are produced on the leaves, the female galls on the branchlets. Both are caused by the insects' feeding, and the duration of the instars appears to depend on the rate of growth of the galls. This is an interesting case, for, although gall formation is ascribed to the effect of feeding egg or larval secretions, this datum suggests that in turn the growth of the gall tissue affects the growth rate of the insect. In what manner is not described. This is contrary to the opinion of Zweigelt (1943) who concluded that with aphid galls the response of the leaf host is for the benefit of the host plant and does nothing to help the gall insect itself.

The suggestion that root and leaf galls in vines due to *Phylloxera* feeding are the result of injection of indole-3-acetic acid into the plant by the insect is the significant contribution of Nyserakis (1946). The effect of this class of compound on plants is so profound that to establish the role of insects in producing and distributing such compounds into plant cells is of extreme importance. Actually the toxins, in what must be extremely minute quantities, are often so effective that only plant hormones can be compared with them in effectiveness per unit of concentration.

Nyserakis (1947) refers to the symptoms produced by these hormone injections as those of court-noué. The recent literature appears to be so confused as to the real nature of this disease, however, that no adequate review is possible in this paper.

This same author ascribed the resistance of American vines and their hybrids to their relatively low sensitivity to the hetero-auxin secreted by the insect. Modification of this sensitivity by environmental conditions probably accounts for variable results recorded.

Phylloxera strains developed for 15 to 20 years on European vines were incapable of developing on American vines, according to Prinz (1937). The ability of such strains to produce galls on American vines returned only when they had developed on the roots of American vines for long periods.

If this last abstract (Prinz) is considered in relation to that of Nyserakis just preceding, it would appear that in order to harmonize the two findings it would be necessary to postulate the development of nutritional strains of the insect which ultimately were well enough defined to produce the appropriate hormone necessary to induce galls on the variety of vine on which the insect itself developed.

Bramstedt (1938) found a positive correlation between the degree of immunity or resistance of apple seedlings to the woolly apple aphid and the characteristic changes which the aphid caused in the attacked tissues. This was true not only of the susceptible gall-forming variety but also of those which showed immunity.

Underhill and Cox (1938) define a variety resistant to woolly apple aphid as one on the roots of which the aphids establish temporary infestations but do not produce or stimulate formation of galls.

Sakimura (1947) has reviewed the literature on gall-forming thrips. They are minor and rather primitive gall formers, with the shape of the galls usually specific to the host plant and to the

thrips species producing it. The same species of thrips produces different shapes of galls on different species of plants, while different species of thrips produce different shapes of galls on the same species of plants.

A very complete study of a gall insect is that of Parr (1940). The problem of gall formation is taken up in some detail. It is clear that this scale (*Asterolecanium variolosum* Ratzeburg) has other effects upon the host tissue than mere withdrawal of cell contents. The sequence of these is as follows: (a) collenchyma of the twig is stimulated and begins to proliferate but not the cells through which the stylets pass or those immediately surrounding; (b) these cells are either killed immediately by the salivary fluids or by the extraction of the cell contents; (c) they may be inhibited from proliferation if not killed. The gall grows in size as the insect grows. The plant tissues surrounding the parasite proliferate radially by both hyperplastic and hypertrophic activity. Effect of the salivary secretion continues, even after the insect itself has gone. Experimental injections with salivary extracts produced galls similar in shape to those caused by the insect. When salivary extracts were heated to 60° C they did not produce galls, suggesting an enzyme-like substance as the cause of gall formation. In Rio de Janeiro, *A. postulans* affects trees similarly³.

Matsucoccus vexillorum Morrison causes girdling lesions on Ponderosa pine (*Pinus ponderosa* Laws.) in the Southwest. It would appear that the damage by this insect is in producing rapid necrosis which becomes associated with many species of fungi and bacteria (McKenzie and Gill, 1948).

Another species (*Matsucoccus bisetosus* Morrison) is an enemy of California pines (McKenzie, 1941).

Parr (1939), studying *Matsucoccus* species in the Northeast, also on pines, described the tissue reaction to the insects' feeding, wherein there is a collapse and disintegration of plant tissue around the base of the stylets, forming a depression into which the 1st instar of the insect feeds. The 2nd instar becomes completely covered by plant tissue, producing a gall. Extracts of salivary glands injected into the plant tissue produced some symptoms typical of the actual damage done by the insect.

Keiffer (1946) has reviewed the economic species of eriophyids

³ Oral communication from Dr. Costa Lima.

and separates them into two general classes, bud mites and gall-formers. Gall formation shows a very intimate mite-host relationship. The grape *Erineum* mite can form galls only on very tiny leaves, but there is a bud-mite development which can cause serious damage without production of any *Erineum* galls. The tendency for some economic gall mites to divest themselves of the gall-making habit and to remain as bud mites is noted by Keiffer who includes a complete list of the economic species with descriptions of the damage done. This includes warty deformations, leaf blisters, hairy deformations, terminal bud galls, formation of *Erineum* patches on the leaf endodermis, stunting and deformation of leaves, formation of pouch galls on upper leaf surfaces, yellowing and dropping of pine needles, formation of woody galls around the buds, conspicuous cell-like galls on leaves, and hairy growths on petioles.

Lewis and Walton (1947) have described a substance which initiates, stimulates and directs development in differentiation in the cells of the cone gall of witch hazel (*Hamamelis virginica* L.). It is injected into the leaf by the aphid *Hormaphis hamamelidis* Fitch. These authors differentiated distinctly between this substance and salivary secretions. They refer to the injection of the specific substances as a process of stinging and state that the substance originates in the glands opening into the stylar canal. Use of the word "stinging" is unusual but perhaps justified to separate the normal process of feeding and the injection of the stimulating substance by the mouth parts. The effect of the sting substance is rapid, and when about 150 stings have been made over a small circular area of the leaf the highly specialized cone gall develops. The injected material is carefully described. When injected directly into the cytoplasm, it is seen as a single globule usually containing one refractory crystalloid. The globule enters the nucleus and then the nucleolus where the crystalloid breaks up into smaller bodies. Whether the injection is intra- or intercellular, the end result is the entry of the crystalloids into the nucleolus. There they may fuse to form a single large crystalloid which breaks up into smaller ones when the nucleus enters prophase. The number of these bodies increases as mitosis approaches, when they are distributed to the daughter nuclei where they are found in the nucleolus as they were in the mother nucleus. Repeated stinging by

the stem mother must continue if the gall is to continue to grow, and only the stem mother can initiate gall formation. The authors look on this gall as a neoplasm induced by a specific substance injected into the plant by the aphid, and produced separately and distinctly from the normal salivary secretions.

Martin (1942, 1938) extracted macerated green leafhoppers (*Draculacephala mollipes*) and injected the extract into three-month-old sugar-cane plants. The result was formation of galls at the internodes with both sterilized and unsterilized extract. Adjacent growing points were also stimulated by the injections. This case again suggests the hormone-like action of the insect injections, but a macerated whole insect is a very complex compound, and it might well be that hormones in some tissues of an insect never reach the salivary glands.

CICADELLIDAE

Injury by leafhoppers includes leaf spotting, the more extensive injury known as hopperburn, and two types of systemic injury, wilting and symptoms closely approximating those of a virus.

Fetola disease of orange is an example of leafhopper spotting. This disease, which results in the disfiguring of oranges by small discolored skin areas, ranging in size from a few mm. to 15–20 mm., has been shown to be due to the punctures of an *Empoasca* species. The disease, known for many years, suddenly became epidemic, and this outbreak apparently coincided with the presence of very large numbers of *Empoasca* in the orchards (Dulzetto and Muscatello, 1939; Vittoria, 1940).

The nature of the injury to alfalfa caused by *Empoasca fabae* has been described by Medler (1941). The feeding punctures of three species of leafhoppers, including *E. fabae*, were compared histologically. There were no apparent internal physiological changes in cells surrounding the punctures made by two of these species, but with *E. fabae* there was hypertrophy in affected cells, characterized by nuclear enlargement and prominent safranin-stained nucleoli. External symptoms of chlorosis and reddening noted by previous workers and ascribed to interference with translocation are shown to be secondary symptoms.

Marshall et al (1942) compared *E. fabae* with species of apple leafhoppers (*Typhlocyba* spp.) and grape leafhoppers (*Erythro-*

neura spp.). The effect of *E. fabae* feeding on leaf metabolism was more pronounced than that of the other species of leafhopper groups with similar numbers of insects involved.

Symptoms of hopperburn may be confused with those of boron deficiencies, according to Colwell and Lincoln (1942). The distribution of discoloration is one of the best criteria. The leaves injured by leafhoppers occur at various heights on a given shoot; the injury is confined to terminal points, possibly including one or more lateral terminals in addition to the main one. There is always a shortening of the terminal internode in plants showing boron deficiency. The terminal bud of a B-deficient alfalfa shoot is always abnormal; that of a shoot injured by leafhoppers may be normal.

E. fabae is considered the most important domestic species of the genus because of the very large variety of host plants on which it feeds, its ability to build up populations rapidly, and its peculiar habit of feeding on the phloem and xylem instead of the mesophyll of the host plant, according to Poos and Wheeler (1943). These workers also found that the disease-like injury caused by this insect is usually characteristic of each species of plant injured, and for that reason the injuries have become known by various names. Specific feeding injuries to rose were described by Smith (1940).

Low fruit yield and small distorted brownish-green foliage on plum trees, first ascribed to mineral deficiencies, were shown by Merrill (1946) to be most probably due to attacks of *Empoasca fabae*.

Quantitative relationships between the numbers of *Empoasca fabae* and yields of potatoes are described by Peterson and Granovsky (1950). Relationship of yield to nymphal density and percentage hopperburn can be expressed by logarithmic curves. A low leafhopper density can produce relatively great yield reductions, but increases above these initial disease-inducing populations do not result in a proportionate amount of damage.

References to potato leafhopper in relation to resistance and susceptibility are available. Allen et al (1940) reported on the influence of planting date on leafhopper populations and hopperburn development. Hopperburn development was greater in the early maturing varieties regardless of planting date but could be reduced by deferring planting date for both early and late varieties.

Nymphal leafhopper population is closely correlated with hopperburn development in respect to time of planting. Planting time is not the prime factor in determining susceptibility or resistance to hopperburn.

Peterson and Granovsky (1950a) compared the relative feeding effects of *E. fabae* on resistant and susceptible potato varieties. Varietal differences in reaction to leafhopper feeding may involve both morphological and physiological characters. The resistant variety, Sequoia, has thicker-walled collenchyma, and its phloem is more extensive and is often of greater distance from the lower epidermis, thus reducing the interference with translocation and the accumulations of carbohydrates as compared with the susceptible Cobbler. There was also some evidence of a varietal difference in physiological response to the toxin injected by the leafhopper during the course of feeding.

Sleesman (1940) noted differences in insect attack by *E. fabae* among 12 species of *Solanum* in Ohio. Four of these species were highly resistant, if not immune, to attack.

Hopperburn resistance in potatoes is the subject of a detailed study by McFarlane (1942). Hopperburn is believed to be second only to virus in importance in the culture of potatoes. Great variation in susceptibility between these varieties occurs. Nymphal populations were counted on field plots, and the most susceptible variety had the highest populations of nymphs. There was no correlation between the number of nymphs and the amount of hopperburn, however. Hopperburn development is affected by other factors. Mosaic disease, for example, increases the susceptibility. The early maturing varieties in general were not susceptible to hopperburn, but stage of maturity is not the effective factor. Crosses of resistant to resistant produced about 90% seedlings in the lowest damage class, and segregation of susceptible and resistant was clear in the F_1 generation.

McFarlane and Rieman (1943) tested 27 varieties of snap and lima beans for resistance to *E. fabae*. In general, the early maturing varieties were more susceptible, while the late maturing ones tended to be resistant.

The study of resistance of cotton plants to *E. facialis* Jac. by Parnell et al (1949) revealed that hairiness and resistance developed concurrently, probably through its effect on oviposition.

Species of the genus *Empoasca* are reported by Sloan (1938) as damaging cotton in Queensland. Result is stunting which, already affected by soil moisture, is accentuated. The leaves wilt and the main terminal shoot becomes distorted. Recovery from this occurs after heavy rains. Infestation of maturing plants by adults and nymphs caused a brownish or reddish discoloration and curling of the leaves. Plant development is retarded and almost ceases without general reddening, and there is shedding of the squares, flowers and young bolls. The injury is believed to be due to a combination of toxic injections and removal of sap. Resistant varieties of cotton are available, resistant plants being typically hairy on the lower surfaces. Length of the hairs appears to be more important than their density.

Empoasca flavescens Fab. prevented the establishment of cotton growing in Luzon (Cendana et al, 1947). On cotton this species caused wilting and drying of the leaves, and infested plants appeared stunted and unthrifty. Other host plants were less susceptible to attack.

Martin and Pemberton (1942) described typical hopperburns on lettuce and celtsuce caused by *Empoasca solana* Del. It was concluded from experimental evidence that a toxic secretion was involved. The degree of injury varied directly with the insect population, and the plants recovered after insects were removed.

Hills et al (1944), however, with the same insect in Arizona, considered the effect on sugar beet seed plants was largely one of devitalization.

Control is achieved by reducing the numbers of leafhoppers. DeLong (1940), in a detailed study of the use of insecticides, reported that immediate results were obtained with various pyrethrum sprays. Bordeaux mixture had an excellent residual effect, believed to be essentially due to absorption of the copper compounds by the plants and to the toxicity of these compounds when insects fed upon them. This effect lasted several days after treatment. Various sulfur compounds were also considered effective control materials.

Whitewash spray of hydrated lime, zinc sulphate and blood albumin spreader has been used against potato leafhoppers in California, but only 37% improvement over untreated orchards was obtained (Woglum et al, 1940).

Miller (1942) reported on control of the leafhopper on peanuts. He recommends application of three or four dusts of finely ground sulfur at two-week intervals. This dusting is reported to control also leaf spot (*Cercospora* spp.) commonly found with leafhopper damage. Poos (1941), however, considered that peanut "pouts" should be referred to thrips as causative, not to leafhoppers.

Wilting of peach seedlings after feeding by the leafhopper *Macropsis trimaculata* Fitch was noted by Kunkel (1933). Ten adults feeding for a week caused sudden wilting of the tree. Death of the tree is avoided if the insects are removed; otherwise the tree dies from the tips downward. Wilting may occur, however, several days after the insects have been removed, suggesting translocation of the toxin from the feeding point. This is the first known case of an insect transmitting a toxin independent of virus transmission by the same insect.

Severin et al (1945) have reported on a most interesting case of toxicity brought about by the feeding of the leafhopper *Xerophloea vanduzeei* Law. The symptoms produced by the feeding of this non-infective individual of this species are so close to those indicative of aster yellows and curlytop that they could well be confused with them. These symptoms on sugar beets include clearing of veins and veinlets, swelling of veinlets, interveinal protuberances on the upper surface of the leaf, inward rolling of the margin and curved midrib, as well as gross yellowed areas and necrosis of midrib and veins. On China aster, vein clearing, asymmetrical leaves and flower breaking with twisted and abnormal petals occur. Transmission experiments failed to recover the disease from affected beets and asters either by means of mechanical inoculations or non-infective adult insects. However, by injection of crushed salivary glands of nymphs and by the feeding of non-infective nymphs, symptoms were produced. There is evidence also that the causative agent is systemic in its effects, since symptoms developed on the youngest leaves when insects had been fed only on the older leaves. Perhaps "systemic" needs finer definition. A toxic agent might be translocated from the point of entry to a point where its chemical affinities permit its toxic action, but the symptoms might still be local. The mealybug striping of pineapple (Carter, 1948) now appears (unpublished data) to be a case in point.

Continuing his inquiry, Severin (1947) described feeding effects

of large numbers of leafhopper vectors of California aster-yellows virus. Ten species of these induced symptoms on asters and celery. A single non-infective nymph induced cleared vein and veinlets with yellow veinbanding on the youngest leaves of healthy celery plants which developed in the advance stages to chlorosis of the inner and intermediate leaves. This was true for two species: *Texananus latipex* DeLong and *Texananus lathropi* Osborn and Lathrop. Other species caused cleared veins and veinlets, followed by either white or yellow veinbanding, mottling and spreading chlorosis. With *Texananus spatulatus* Van Duzee the symptoms vary according to the populations of the leafhoppers. Stunting and curving of the petioles of the younger leaves of healthy celery plants follows the feeding of adults of *Gyponana hasta*, a symptom which is lost from the newly developing leaves when the leafhoppers are removed. A single nymph of *Idiodonus heidemanni* (Ball) will induce yellow discoloration. These yellow areas increase in size and are followed by necrosis.

CERCOPIDAE

Research on froghopper blight of sugar cane has been summarized by Pickles (1942). Improved agronomy, i.e., cultivation and manurial practices, have reduced the effects of mild infestations; but when outbreaks are severe, control measures are necessary. The same author (1940) has reported on the control of the insect by dusts. A combination of pyrethrum and sulfur dust, blown through the sugar cane at great speed, has resulted in 80 to 90 per cent control. Granted that only large estates can use this method, it is one of the few large-scale tropical insect-control measures by means of chemicals which have been achieved. The same author (1942) recommended use of Cyanogas for nymphal destruction and pyrethrum if later destruction of the adults was necessary.

With the advent of the new organic insecticides, Pickles (1946) was able to propose that DDT in not less than 4% concentration, Sabadilla in 30% concentration, and mixtures of the two insecticides are able to reduce froghopper populations of 30 to 50 adults per stool to a level at which economic injury to sugar cane does not take place.

Caminha (1944) reports on another species (*T. liturata* var. *ruforibulata*) on sugar cane in Brazil. This species is injurious

apparently only in the nymphal stage when it feeds on the roots. The adults are reported causing little injury to the leaves. This is in contrast to the sugar-cane froghopper (*Tomaspis saccharina* Dist.) of Trinidad, which causes definite lesions of the leaves. Caminha reports that nymphal colonies of up to 50 per plant have been observed, and that colonies of this size reduce the sugar content of the cane and produce fragile pale plants.

Juantorena (1950) states that gammexane, DDT and mixtures of the two give good results against *Tomaspis boedkini* in Venezuela.

James (1946) concluded that with populations of less than ten adult froghoppers per stool of cane it is not economical to attempt to control *T. flavilatera* Ur., the sugar-cane froghopper in Demerara.

PSYLLIDAE

Two important papers on psyllid yellows (Hartman, 1937; Schaal, 1938) were inadvertently omitted from the previous review. Hartman observes that the relation of wild host plants to psyllid abundance is important, the preferred hosts being in the family Solanaceae, both wild and cultivated, but also the native red cedar. Hartman makes one reference which appears to confirm Daniels' statement (1934) that psyllids are sometimes present in large numbers without the disease being present. Hartman says: "As soon as one field in a given community was found to be infested . . . they could be found some place within nearly every field in that same locality. . . . It was also found that after infestation by psyllids occurred, . . . some fields readily developed psyllid symptoms. . . . At the same time other fields in the same community developed few or no symptoms. . . .". These statements suggest that there are differences in psyllid colonies or that susceptibility varies greatly between fields in the same locality. Hartman has observed no reactions to psyllid feeding before the potato is in the budding stage.

Factors affecting symptoms are described by Schaal (1938). Symptoms are more pronounced when the psyllid population is high and will first appear in the field as a bronze coloration. The underground symptoms are expressed by an abnormally large number of stolons and root development. Tubers are usually small and very numerous. This results in a great reduction in

marketable tubers and sometimes in the abandonment of fields before harvest. That the disease has interfered with translocation is indicated from the almost starch-free condition of the tubers, while the aerial portions of the plant are high in starch. Symptoms varied in seedling varieties. In some, development of small tubers was greatly increased, with few top symptoms; in others the converse occurred. Schaal found a definite relationship between numbers of nymphs and the severity of symptoms, but he noted no further increase when more than 100 nymphs were used. Interrupting the feeding of the insects by knocking them off the plants with a water stream reduced the total mass-feeding effect and thereby the severity of symptom expression. No tuber transmission was obtained, but plants grown from infected tubers were less vigorous than those from normal tubers.

Schaal also records successful experiments on the production of symptoms by injection of extracts of ground-up nymphs. The more concentrated extract gave the most typical color symptoms. It is interesting to note that curling and yellowing of the leaves, normally showing six to 14 days after first color symptoms (*ibid.*), did not appear in the injected plants until the injected plants started to form stolons. No progress has been reported on the most interesting aspect of the etiology of the disease, namely, the difference between the ability of nymphs and adults in inducing the disease. There is a decided challenge to experimenters to determine the difference in the adult and nymphal secretions, but this may be beyond available experimental techniques.

Potatoes grown in highly alkaline soil (pH 8.4), or infested with fungus diseases, or injured mechanically in the stems and root systems developed symptoms of psyllid yellows with fewer insects present than when the plants were growing normally.

Edmundson (1940) compared the yields from seed produced by parent plants following different degrees of psyllid injury. The size of plants and yield of tubers were reduced according to the severity of the psyllid injury of the parent plants.

Spindling sprout of potatoes (hair sprout), ascribed to several more or less tangible causes by many authors, has been experimentally demonstrated by Snyder et al (1946) to be a phase of psyllid damage. There are presumably other causes or some other toxicogenic insect responsible for the occurrence of spindling

sprout in areas where the tomato psyllid does not occur. The suggestion is made that the virus purple top may also have spindling sprout as a symptom.

Spindling sprout was not tuber transmitted, and there is no evidence for involvement of a virus. Plants grown the first generation from diseased tubers yielded only one-half that of normal potatoes, but in the second generation recovery was complete and yield normal.

Internal necrosis as a symptom of psyllid yellows was first reported by Sanford and Grimble (1944) as occurring in Canada. Snyder et al (1946a) report a similar type of phloem necrosis in spindling sprout tubers, but their evidence indicates that this symptom follows only very heavy infestation and storage of the tubers.

Harvey et al (1944) studied the physiology of hair sprout without any specific reference to causal entity. With the material they used, the total sugars and reducing percentages were increased and the percentage dry weight decreased over normal tubers of White Rose potatoes. These differences in sugar content were maintained at high and at low storage temperatures. Differences in the percentage of starch were insignificant.

Michener (1943), in an attempt to determine the physiological nature of spindling sprout, grafted spindling sprout scions on normal stalks, and vice versa. The spindling sprout stems increased in size when grafted on normal stems, suggesting that the spindling sprout stems lacked normal growth materials which they derived from the normal stems or that translocation of the necessary growth substances was interfered with so they could not be transported to the growing stem of the spindling sprout.

The nature of spindling sprout has been investigated by Parris and Jones (1941), using seed potatoes imported to Hawaii from North Dakota as experimental material. Chemical analyses showed that spindling sprout tubers contained more reducing sugars, sucrose, acid-hydralizable materials, soluble nitrogen, ammonia and amino-nitrogen than was found in normal tubers. The difference in concentration of reducing sugars and sucrose was considered significant. While plug grafting with spindling sprout cores did not transmit spindling sprout, the eyes of normal tubers were stimulated by core grafting with spindling sprout cores, and the yields from such normal tubers were greater than those from

normal ungrafted tubers or normal tubers grafted with normal cores.

While spindling sprout has been ascribed to many causes (Schultz, 1939), the evidence that it is a concomitant of psyllid yellows makes the possibility of considering insect toxins as having hormonal effects a very interesting and significant one. The permanence of such effects may vary without vitiating the hypothesis. Spindling tubers apparently do not recover with at least two generations of growth, and it is possible that similar conditions may actually leave permanent effects on vegetatively reproduced plants. Separation of such cases from those of vegetative transmittal of viruses would present some technical difficulties.

Hill (1947) records the weather sequence associated with heavy psyllid damage in Nebraska. An unusually wet July was followed by two hot and dry months which permitted optimum temperatures for development, even though the vine growth was dense and provided shade.

Wallis (1946), in a paper on the ecology of the insect, suggests that it may migrate into areas where it does not overwinter. Romney (1939) found that movements of the insect coincided with those of the sugar-beet leafhopper, and that probably the Rio Grande drainage area serves as a source of infestation east of the Continental Divide as far north as Colorado.

Pletsch (1947) has a detailed account of the insect's biology. Included is an account of feeding the insects on radioactive ($P^{32}O_4$) tomato plants. Although the insects became "loaded" with radioactivity, and excrement and exuvia were also positive for radioactivity, there was no evidence that the nymphs injected any radioactive material into new healthy leaflets to which they were transferred. It is possible, of course, that the radioactive component taken up by the insects did not return to the salivary glands, nor that it was regurgitated. Obviously the insect does inject salivary secretion into the plant.

Immunity from psyllid attack has been found, but considerable differences exist in the relative susceptibility (Babb et al, 1944) of varieties and seedlings, and these differences are less pronounced in years of heavy outbreaks.

Control of psyllid yellows is achieved by reducing the populations by spraying or dusting. List (1939, 1943) used sulfur,

either as dusting or wettable sulfur and as lime-sulfur, to repel adults and kill nymphs. Riedl (1943) considered 325 mesh dusting sulfur more efficacious than either lime-sulfur or wettable sulfur sprays. Pletsch (1942) reported that all forms of sulfur used were effective against 1st instar nymphs. Swenk and Tate (1940) emphasized effective timing of sprays if good control is to be achieved, and they recommend a protective spray when the plants are six or eight inches above ground. After that spray, further spraying should be determined by inspection for the presence of nymphs. Riedl and Harrison (1945) described combinations of sulfur and fluosilicates as the most efficient insecticides available against psyllids.

Pussard (1939) has determined that the salivary glands of adults of three species of *Psylla* contain diastase which converts starch into soluble carbohydrates.

Heinze and Profft (1939) got no transmission of virus by *Trioxa nigricornis* Frst., but leaves infested with a large number of nymphs showed slight curling, light colored spots on the underside and red discoloration of the leaves. No symptoms were caused by adult feeding, and the tubers from plants injured by the psyllid gave rise to plants that displayed no symptoms.

MEALYBUGS AND SCALE INSECTS

Carter (1949) reported a dark-brown circular scale insect (*Melanaspis bromeliae* Leonard) on pineapple plants at Deodoro near Rio de Janeiro. The insect was associated with a curious and previously undescribed spotting of the leaf. Underneath the scale, the color of the leaf is darker than the normal color. This darker-green spot is circular. A much larger chlorotic ring forms a halo round this spot. Development of the dark central ring begins shortly after establishment of the crawler on the leaf. The chlorotic ring develops later and becomes depressed, leaving the green center as an elevated island.

The scale insect (*Lecanium coryli* L. causes death or severe damage to ash trees. The symptom sequence has been described by Komarek (1946) as being brought about by the feeding of adult females only. For a short period after the final moult, these adults feed vigorously and increase in size 11 to 15 times. From histological studies it has been shown that the action of the saliva be-

comes apparent round the tips of the stylets; later the cells along the stylet track become brown. The cell walls are then destroyed, presumably by the action of cellulases in the saliva which then penetrates the adjoining cells. Cork tissue is formed through the cambium, and in heavy infestations this results in cutting the vascular tissue off, with resulting dieback of twigs and branches. The histological evidence in this case is important, since otherwise the corking of the cambium, actually a very secondary symptom, would probably have been ascribed to mechanical injury only.

Heriot (1944) questions the assumption that scale and aphid infestation injury is mainly due to extraction of the sap but at the same time points out that as a scale feeds, the stylets are broken off at each moult and left imbedded in the bark and cambium. These obstructions in the tissues are accumulative and permanent.

Pseudococcus adonidum L. produces very well-defined chlorotic spots in pineapple leaves in Queensland. Similarly Diaspine scale was found in Fiji where it produced very large, almost one cm. wide, chlorotic white spots on pineapple leaves (Carter, 1942).

Mealybugs on cacao produced interesting feeding effects. A gross colony of *Pseudococcus citri* Risso from jack fruit (*Artocarpus integrifolia*) killed the growing point of cacao seedlings and induced adventitious budding. Single mealybugs caged on young leaves near the growing point, however, resulted first in an abnormal "witches broom" effect of the bud; and, when the new leaves emerged to a length of a few centimeters, they became brittle and could be flicked off with the finger. Since *Pseudococcus citri* was found on other cacao plants in the Rio Botanic Garden but with no symptoms evident, the experiment indicated that *P. citri* from the jack fruit had injected specific oral secretions. The initial effect was clearly one of inducing leaf abscission (Carter, 1949).

Green spotting by *Pseudococcus brevipes* Ckll. was recorded by Carter (1942) from many places throughout the world. Discovery of green-spotting *P. brevipes* strains in East Africa and Malaya without the typical symbiont flora of the Hawaiian green-spotting strain involved abandonment of the hypothesis that the rod-like symbiont is causally related to green spotting (Carter, 1942).

Experience indicated, however, that green-spotting strains in Brazil were bisexual as in Hawaii and contained rod-like symbionts in their mycetomes (unpublished data). Mealybug colonies

in Brazil, however, appeared to be more characteristically sub-surface than aerial.

Feeding injury by mealybugs was discussed by Glass (1944). He concluded that *Pseudococcus comstocki* Kuw. and *Phenacoccus colemani* Ehrh. fed on the phloem and xylem, and that there is localized breakdown in cells of these tissues, but no other effect besides what might be anticipated after withdrawal of plant foods.

Schoene (1941), in a discussion of plant fertilization and mealybug injury, related the latter to the physiological status of apple trees in a manner closely comparable with that described by Andrews (1923) and discussed in some detail in the previous review (Carter, 1939). In a practical way it involves a relationship between mealybug infestation and fertilization practice in the Virginia apple orchards. Schoene concluded quite properly that the evidence of his paper points to the desirability of investigation on the effect of plant food on insect injury to plants.

Mealybug spotting of strawberry plants (Hildebrand, 1939) closely approximates the symptoms of a virus disease, known as crinkle. The chlorotic circular to irregular spots are apparently formed by mealybug feeding in the curled young leaves; but as they grow older, mottling and dwarfing develop, especially on the more heavily infested plants. The translucent spots are the sites of feeding punctures, but the mottling and dwarfing must clearly be either secondary effects of large numbers of punctures, analogous to slow wilt of pineapples, or caused by some diffused and translocated fraction of the insect's secretion.

Priesner (1939), in a discussion of relationships between scale and mealybug infestations and the physiological condition of the food plant, points out the influence of physical variations in the food plant on these insect species. The physical condition of the cell sap is believed to be as important as its chemical condition in the case of certain insects. He relates this to the osmotic pressure of the cell sap.

Localized toxic effects due to translocation of the toxic entity have already been referred to by Severin et al (1945) in connection with toxic leafhopper feeding. The striping of pineapple leaves by *Pseudococcus brevipes* follows in this same class. Carter (1944) stated that these symptoms appear on a short section of each leaf at approximately the same level on the leaf. The first

examples seen and described had evidence of feeding within the affected area in the shape of typical green spots. Unpublished data, however, show that this symptom occurs on tissues considerably removed from the feeding point of the insect, suggesting translocation of the symptom-producing entity to some susceptible tissue, probably meristematic. That this symptom is not related to mealybug wilt is indicated by the fact that the standard Cayenne pineapple variety susceptible to mealybug wilt has never shown symptoms of mealybug stripe, and the long feeding on agar which has been shown (Carter, 1951) to eliminate the wilt-producing capacity of mealybugs does not appear to affect the ability of the insects to produce mealybug stripe on susceptible seedlings (Carter, 1945). This symptom has been noted very rarely on pineapple plants also in Brazil (Carter, 1949).

With the increased interest in pineapple growing in many parts of the world, distribution data on mealybug wilt are of significance. Jepson and Wiehe (1939) report that in Mauritius mealybugs were known on pineapple long before any development of plantations on an economic scale, but they did not attract attention. With increase in cultivated areas, however, mealybug populations rose, and with this came serious wilt disease.

Westgate (1945) records mealybug wilt and low temperature as the two major problems of pineapple growing in Florida. In Puerto Rico mealybug wilt is believed to have caused the abandonment of formerly high producing areas (Plank and Smith, 1940). This last seems contrary to the statement by Jepson and Wiehe that the disease is practically unknown there, but Jepson no doubt refers to the Red Spanish variety which is highly resistant. Smooth Cayenne in Puerto Rico is difficult to maintain on account of its susceptibility to mealybug wilt, and this is true of all the Caribbean countries.

Takahashi (1939) described the presence of mealybug wilt in Formosa. Corbett and Pagden (1941) record the occurrence of mealybug wilt and its experimental demonstration in Malaya. Carter (1942) has recorded the incidence of mealybug wilt over a wide geographic range. Positive determinations were made in South and East Africa, in Malaya, in the Philippines, Australia and Fiji. In a few localities, Laurence Marques and Zanzibar in East Africa, and in Java, Bali and Borneo, no positive cases were

seen in native pineapple plantings, but in all these areas mealybug colonies were small, although quite generally distributed. In Brazil and other South American countries (Carter, 1949) mealybug wilt was found to follow the same general pattern as in other tropical countries, namely, rare in temporary plantings in virgin soil, more common in established pineapple districts, but nowhere as severe as in Hawaii where pineapples of a susceptible variety are grown continuously on the same land.

Factors affecting the incidence of the disease are reported by Corbett and Pagden (1941) who note the prevalence of wilt in pineapples grown in the lateritic mineral soils as compared with peat soils, and recommend that new plantings be restricted to peat soils. Healthy pineapple plants in Malaya, according to these authors, are to be found principally in the newly opened (i.e., virgin) peat soils. The influence of heavy rains in reducing leaf populations and favoring establishment of sub-surface colonies is also noted as a factor in minimizing wilt incidence generally in Malaya. Carter (1942) noted that in pineapple growing on the fringe of the plant's economic range, low temperatures materially reduced the size of mealybug colonies and that, although these are quite generally distributed, wilt incidence was low. Lands rich in organic matter, as in Zanzibar, showed little evidence of wilt—in fact, only dubious cases were recorded. On the adjacent East African mainland, however, in soils deficient in organic matter and with higher temperatures prevailing, mealybug wilt was a limiting factor, and these areas have since been abandoned. Again in the highlands of Kenya at 5,000 feet altitude, mealybug colonies were small and wilt rare. These latter localities, however, were on virgin soil, and more recent information is that with older plantings, wilt has increased. Native plantings, that is, the few isolated plants usually in partial shade around the grower's house, were of a rough native variety, and under these circumstances no wilt was found.

The incidence of the disease in the State of São Paulo in Brazil (Carter, 1949) is of interest. Planting material was found to be almost universally infested with a few mealybugs on the base of the slip. Mealybug colonies were for the most part confined to the base leaves under the surfaces of the soil; upper-leaf colonies were rare. Wilt incidence seems to be associated with the movement of

mealybugs up from these base-leaf colonies to the inner leaves of the plant.

If only the size of the mealybug colonies in the São Paulo area were considered, the losses from mealybug wilt would be unaccountably low. However, the colonies are for the most part base-leaf colonies. There has been a movement of pineapple growing from one locality to another for various reasons, so that the culture of pineapple there has been essentially on virgin land in spite of its 50-year history. Pineapple planting material and, of course, the accompanying mealybug infestations have moved with the transfer from one locality to another.

In the State of Pernambuco, where more tropical conditions obtain, wilt is more common in spite of the fact that the variety grown there, known as White Paulista (Pernambuco), is more resistant than the Yellow Paulista variety of the South. In this State exceptions to the general rule that virgin lands are free from wilt were found in some of the coastal areas with very poor sandy soil. On the other hand, one comparison was available which supported the generalization, even there. An area planted to pineapple, all of the same age and development, showed wilt to be much more prevalent in one-half of the field. That was a replanted section; the other half was virgin, following forest. The two sections had been planted as one with the same source of planting material and the same agronomic treatment after planting. Scattered native plantings, usually wilt-free, were found to be wilted also in Dutch Guiana where the soil was impoverished and appeared to be little more than pure quartz sand.

Symptoms have been described by Jepson and Wiehe (1939) as having different expression in summer and winter in Mauritius. In summer the symptoms appear to be identical with those described from Hawaii. The winter symptoms are primarily those of dieback, with chlorotic leaves, the outer leaves becoming mottled with areas of yellow and green. Both types of symptoms, which do not overlap seasonally, are ascribed to *P. brevipes* feeding.

Carter (1945c) has listed five stages in the progression from first symptoms: a preliminary reddening of the leaves—through to the fourth—most severe stage; then to a recovery stage which is first observed when the center leaves regain their turgidity and grow out apparently normally. There are, however, some other expressions of symptoms. Occasionally one or two leaves only

will show symptoms, and these may develop to any one of the first three stages. Sometimes this limited initial expression may develop to typical all-over third stage, but in others no further development occurs. The limited symptom expression occurs more frequently in field-grown plants infested after they are over nine months of age. There is a fair percentage of plants which show only the first-stage symptom and recover from that very rapidly. It is extremely likely in view of this, that many plants are injured without expression of visible symptoms, and this has been shown in reduced plant weight and lower production of slips and suckers (Carter and Collins, 1947).

Symptoms thus far discussed have been leaf symptoms, but the root symptom, not of course normally seen, is actually the first symptom. Carter (1948) has shown that the first symptom is cessation of root elongation, followed by soft collapse. The period for development of root symptoms closely approximates the time required for radioactive phosphorus injected into the plant by mealybug feeding to reach the roots (Carter, 1945).

Leaf symptoms follow these root symptoms. New roots emerging afterward are normal and are associated with recovery of the plant. The method used, that of growing plants in water vapor boxes which permitted ready examination of both roots and leaves at any time, greatly facilitated detailed measurements of symptoms and measurement of feeding effects difficult to achieve in field plants (Carter, 1942a).

In this manner it was possible to determine the relative effect of repeated infestations with small populations with and without intermittent spraying. None of these small increments caused wilt singly when tested on field check plants; but when three of these ten-bug lots were applied but sprayed out after each had had two weeks feeding, the symptom developed on both root and leaves was very much less than when the second and third lots of mealybugs were added to the first without intermittent spraying.

Period for development of symptoms varies. In a population of 6,526 wilted plants, infested when five months old, the period varied from 43 to 125 days, with the peak at 70 days. In a population of 1,295 wilted plants, infested when nine and one-half months old, the period varied from 56 to 295 days, with no distinct peak period.

Symptom expression in varieties and hybrids varies (Carter and

Collins, 1947). The amount of anthocyanin affects the development of red and pink in the leaves. The 3rd-stage wilt is more definite in the broader succulent-leaved varieties than in those with narrow stiff-leaved varieties.

Symptom expression in a resistant hybrid, 7898, is of great significance. Symptoms range from a slight yellowing of a few adjacent median leaves to symptoms typical of those in Cayenne in every respect except for the development of red and pink color (the hybrid is practically anthocyanin-free) and with only rare development to 4th-stage wilt.

It is in the relationship between mealybug feeding sequence and symptoms, however, that special significance lies. When this variety is infested with mealybugs from Cayenne, the slight yellowing symptom is the typical reaction, if any occurs. The incidence of this symptom in 7898 was, however, greatly increased by infesting the plants successively at monthly intervals; and in addition, in the more frequently infested plants, later drying up of the fruit peduncle and consequent falling over of the fruit occurred.

This mild and often transitory symptom followed heavy infestation with mealybugs from the more susceptible Cayenne. Infestation of mealybugs from the same 7898 clone, however, resulted in symptoms typical in every respect of those of Cayenne, except the increase in red and pink color. This phenomenon was first noted in the natural infestation of young 7898 growing next to an older wilt-free but infested ratoon field of the same hybrid and was confirmed by infestations in experimental plots. In the same experiment mealybugs from 7898 applied to Cayenne wilted the Cayenne more severely and in a shorter time than did mealybugs from Cayenne to Cayenne.

Recovery from wilt is typical when young plants are wilted, for in general the earlier a plant is wilted the more likelihood it will recover. When plants wilt in the fruiting stage or when ratoon plants wilt, real recovery is rare, although dormant buds on the stems of both mother stump and ratoon stumps will remain viable.

Recovery is affected by the intensity of the original infestation. Plants wilted by successive infestations recovered much more slowly than those which wilted after being infested only once. Recovered plants are susceptible to wilting a second time, and adverse growing conditions increase susceptibility to a second wilting (Carter, 1945*b*).

The resistant hybrids and resistant clones of Cayenne available for these studies have shown one remarkable characteristic, more or less in common to them all, and that is their value as positive source plants⁴ in comparison with susceptible varieties or clones. The writer knows of no comparable case, either in plant virology or in any toxin disease known. Only 7898 has been adequately tested in a hybrid-to-hybrid feeding sequence, but, as has already been shown, that clearly resulted in more pronounced wilt than when positive Cayenne bugs were used. Even with mealybugs from 7898 there is evidence that when the colony is developed on the plant, they are more effective than when fed only for a period as long as nine days (Carter, 1951, Table 6), and even 7898 bugs show the same relationship between numbers used and wilt resulting.

Influence of the soil microenvironment on susceptibility to wilt is strongly suggested by the situation on virgin lands, but this factor is obvious in all field experimental plots. The results from one large-scale field experiment are diagrammed by Carter (1945a). No experimental hypothesis is available to account for this phenomenon.

During the years of study, occasional data have accrued that appear to suggest a virus instead of toxin etiology for mealybug wilt. These have been collected in the most recent paper which, although actually published after the end of 1950, is appropriately reviewed here (Carter, 1951).

Mealybugs from wild hosts, i.e., grasses, failed to induce wilt in pineapple plants, although replicated tests many years earlier (Carter, 1933) had shown a low percentage of wilt from these sources. *Yucca* (*Yucca gloriosa* L.) also proved to be a negative host.

Transfers of mealybugs from positive source hosts to an intermediate feeding on negative host plants resulted in failure to induce wilt on test plants, indicating that the last feeding prior to transfer to test plants is determinative. Artificial feeding on agar with and without standard nutrients also resulted in a loss of wilt-inducing capacity. There were a few exceptions to this when the mealybugs

⁴ Positive source plants are those which confer on mealybugs feeding on them the ability to induce wilt in test plants to which the insects are transferred. Feeding on negative source plants does not confer this ability.

were fed on tomato-juice agar, and this finding is worthy of extended study. Transfers from negative hosts to an intermediate feeding on positive source plants, i.e., resistant hybrids and clones of Cayenne, resulted in wilt in the test plants.

The resistant clone or hybrid has been established as the best positive source, although even these are not consistent. Their use has, however, materially reduced the variability in results, which follows the use of mealybug colonies collected from infested and wilted areas of Cayenne. Collections from these areas have shown an extremely wide variation in their ability to induce wilt. The most significant result recorded in this last paper (Carter, 1951), however, is the failure of seedling pineapple plants, with no history of mealybug feeding, as positive sources. Mealybugs fed on these and then transferred to test plants have thus far failed to induce wilt in these test plants.

It is reasonably certain that the resistant clones of Cayenne and the resistant hybrids had been infested many times in their previous vegetative history, but the plants used in these tests as source plants were free of any obvious symptoms. Furthermore, all these positive source plants are themselves susceptible to wilt with suitable mealybug infestations. If, therefore, a virus etiology is involved, as the data could suggest (Carter, 1951), then it is a latent virus. It is difficult to conceive of a plant being a symptom-less carrier and a symptom-bearer of the same entity, so the most reasonable hypothesis is that mealybug wilt might have a latent virus precursor, in the presence of which the toxic secretions of the insect are effective in inducing the disease. Even this hypothesis, however, if later proved, would require to be harmonized with the evidence of localization of wilt which occurs typically in field plots.

Mealybug wilt shares with some other insect-induced disease the favorable circumstance that control is achieved after establishment of the insects on the susceptible host plant (Pickles, 1942; De-Long, 1940; Miller, 1942; Jepson and Wiehe, 1939; List, 1943; Pletsch, 1942).

Osburn (1949) has described the use of parathion dust for control of pineapple mealybug. The chemical, however, reaches only the insects on the leaves, not those under the soil surface.

Wolfenbarger and Westgate (1946) describe experiments with DDT and HCCH (BHC) but did not carry the experiments to

the point of determining the effects of these compounds on development of wilt. Their results with ant control, however, are in line with those obtained in Hawaii.

Treatment of planting stock is described by Osburn (1945) and by Wolfenbarger (1949). Osburn used methyl bromide. Wolfenbarger confirmed Osburn's results on methyl bromide and, in addition, used dips containing parathion wettable powder.

Control methods in Hawaii can not entirely eliminate mealybugs, and small colonies are fairly well distributed throughout pineapple fields. There is, furthermore, no doubt that if these small established colonies are allowed to build up or be maintained for any length of time, wilt will ensue.

The current control of mealybug wilt in Hawaii, however, is probably without precedent in the whole field of insect-induced or insect-transmitted diseases. Whereas formerly field edges and sometimes huge areas were wilted completely before the ratoon crop matured, it is now possible to traverse miles of field road around the edges of pineapple plantations without encountering wilt. Carter (1950) discussed mealybug control methods currently in use in Hawaii.

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Suggestions for the Classification and Nomenclature of Fossil Spores and Pollen Grains	DIVYA DARSHAN PANT <i>University of Allahabad</i>
Comparative Physiology of Gramineous Plants in Relation to Nitrogen	K. N. LAL and M. S. SUBBA RAO <i>Banaras Hindu University</i>
The Telome Theory	CARL L. WILSON <i>Dartmouth College</i>

